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Factors Affecting Germination of Chaparral Seeds

Jon E. Keeley

Abstract.—Factors affecting germination of chaparral seeds by Jon E. Keeley. *Bull. Southern California Acad. Sci.*, 83(3):113-120, 1984. Seedling establishment is uncommon under mature chaparral but abundant after fire. Germination from soils collected beneath chaparral and in an adjacent burned site were compared after various treatments. Application of an aqueous leachate from the dominant overstory shrub (*Adenostoma fasciculatum*) failed to produce any inhibition of seedling emergence from the mature chaparral soil but rather increased germination. Soil heating and powdered charred wood (charate) stimulated germination of dicots but not grasses. Tests of specific species showed *Phacelia cicutaria* and *Salvia columbariae* markedly stimulated by charate whereas *Cryptantha muricata* and *Lotus salsuginosus* were not. Grasses were abundant in the burn soil and germinated readily without treatment; their residence time in the soil, however, may be limited as they were uncommon in the mature chaparral soil. Light was a significant factor in germination of both monocots and dicots. Continuous darkness significantly reduced germination over a 12 hour photoperiod at $\sim 230 \mu\text{E m}^{-2} \text{s}^{-1}$ or $\sim 20 \mu\text{E m}^{-2} \text{s}^{-1}$ or periodic (several hours/week) light of variable intensity.

Chaparral is an evergreen scrub vegetation which dominates much of the undeveloped landscape in southern California. Widespread wildfires are relatively frequent in chaparral due to the dry fuels (resulting from the mediterranean-climate summer drought) and the dense contiguous nature of the vegetation (resulting from the winter and spring rains which are coincident with mild temperatures). Today, man supplies the ignition source for the vast majority of wildfires, though lightning-ignited fires are not uncommon (Keeley 1982). Wildfires are thought to have played a major role in the evolution of chaparral, as the shrubs exhibit a number of adaptations which have been interpreted as evolutionary responses to fire; e.g., seedling recruitment largely restricted to the first postfire year and sprouting from specialized basal burls.

Herbaceous species are generally uncommon in mature chaparral, however, they dominate the post-fire environment for one to several years (Hanes 1977; Keeley et al. 1981). The presence of many of these herb species on recently burned sites is due to seeds dormant under the chaparral and dating back to the previous fire.

Two classes of theories have been proposed to account for relatively depauperate shrub and herb seedling establishment under mature chaparral, but abundant recruitment after fire. Seeds of these species are either 1) inhibited from germinating by chemical components of the environment (e.g., allelopathic substances produced by the overstory shrubs or microbial by-products produced in the litter), or 2) the seeds are refractory and require a stimulus from fire (cues that may stimulate germination include heat, which may crack hard seed coats or melt waxy coverings, and chemical stimulants released from charred wood).

The evidence for chemical inhibition of seed germination under the shrub canopy is not compelling. Sweeney (1956) found that a leachate made from chaparral litter had no inhibitory effect on the germination of various native seeds. McPherson and Muller (1969) could only demonstrate inhibition on four native seeds and only after scarifying them and applying a highly concentrated ($10\times$) leachate from the *Adenostoma fasciculatum* shrub canopy (names according to Munz 1974). Christensen and Muller (1975) found that a leachate from *Adenostoma* did inhibit the germination of two native and two non-native chaparral herbs but had no effect on six of the more typical "pyrophyte endemics." Kaminsky (1981) suggested microbial toxins produced in chaparral soils could inhibit germination of native herbs and demonstrated such an effect on lettuce seeds. Also, he found that soils from a second year burn showed no inhibitory effect. Recently Pack (1985), using native herb seeds and 6 mature and 6 burn soils, was not able to duplicate Kaminsky's results.

Attempts to demonstrate that fire-related cues play a role in stimulating germination have likewise produced conflicting results. Sweeney (1956) found that excelsior burned on top of soil did stimulate germination of native herb seeds but attempts to attribute this to either a chemical product from burned wood or heat were unsuccessful. Likewise McPherson and Muller (1969) and Christensen and Muller (1975) were unable to demonstrate heat stimulated germination of herbs although the latter study as well as others (e.g., Stone and Juhren 1951; Hadley 1961; Quick and Quick 1961) have shown heat stimulated germination of shrub seeds. Although Sweeney (1956) could not demonstrate any effect of ashed wood products, Wicklow (1977), and later Jones and Schlesinger (1980), demonstrated that partially charred wood stimulated germination of *Emmenanthe penduliflora*.

It is clear that no single study is likely to completely clarify the situation. The purpose of this study is to extend these previous investigations to examine how "allelopathic leachate," charred wood and heat affect germination of seeds from natural chaparral soils. In addition, the role of light, which has previously been ignored, was investigated.

Methods

The top 2–4 cm of soil was collected (in early fall) either from beneath mature chaparral (~75 yrs as determined by ring counts) or an adjacent burn (after the end of the second year of regrowth). These sites were in the San Gabriel Mtns. at 900 m, 1 km north of the Monte Cristo Ranger Station. Soils were sieved with a 3 mm screen and the few seeds that did not pass through were added back. The soil was spread to ~3 mm depth on a tray and heated in a forced convection oven at 80°C for 2 hrs or 120°C for 5 min. Petri dishes (100 × 15 mm) were filled with 50 cc of this soil and leachate or charate (see below) treatments were applied.

Leachate from *Adenostoma* foliage was prepared as described by McPherson and Muller (1969). Branches from the upper canopy were cut and placed in a 1 m² funnel and 3 liters of deionized water were applied in a fine mist over a period of 2 hrs. The concentrate was prepared by warming and stirring leachate on a hot plate, maintained below 50°C as suggested by McPherson and Muller (1969).

Charate was prepared from *Adenostoma* wood by charring stem segments with

a torch and grinding in a Wiley mill to pass through a #20 mesh screen. Approximately 2.5 g of powdered charate were applied per dish.

For dishes receiving the leachate treatment, 25 ml of leachate were added. Charate treatments received 27 ml of deionized H₂O, and 25 ml dH₂O were added to all other dishes. Dishes were stacked on trays and covered with black plastic bags to reduce evaporation. The material was then incubated at 5°C for 1 wk, followed by 23°C for 1 wk; and this cycle was repeated two times for a total of 6 weeks. The seeds of four herb species were then added and incubated in the same manner.

In these experiments seeds were incubated in the dark but were exposed to several hours of light each week when germinated seeds were scored. An additional experiment, using some of the treatments described above, was done with seeds in continuous darkness for 6 wks (scoring was done under a green light) or under a 12 hr light regime. The latter dishes were covered with clear plastic bags and placed 150 mm beneath fluorescent lamps where they received ~230 μE m⁻² s⁻¹.

The two soils, as well as a commercial potting soil (for comparison) were analyzed for major inorganic nutrients by an outside commercial soil testing lab.

Results

Fertility of the soils from mature and burned chaparral are compared with a commercial potting soil in Appendix I. Relative to the potting soil, both chaparral soils were markedly depauperate in several important elements. The major soil changes after fire included an increase in pH, Na⁺, PO₄⁻ and CO₃⁻² but a decrease in NO₃⁻.

The buffering capacity of all soils was similar with respect to *Adenostoma* leachate. For example the pH of this leachate varied from 3.5 to 3.8, dependent on concentration. When added to either soil, leachate lowered the pH of the soil solution by 0.1 pH unit. Charate had a pH of 7.4 and when added to burn soil it did not change the pH of the soil solution, but when added to the mature soil the pH increased from 5.6 to 6.0. Since the organic matter was largely broken down in the burn soil it tended to absorb much less water and thus these soils tended to be wetter. Because of this difference it is possible that seeds were exposed to different osmotic pressures in the two soils. Circumstantial evidence suggests

Table 1. Germination from soil collected beneath mature *Adenostoma* chaparral and in an adjacent second year burn (n = 84).

		Seedlings/50 cc soil								
	Soil	Control	1 × Ade- nostoma leachate	4 × Ade- nostoma leachate	Ade- nostoma charate	80°C (2 hrs)	120°C (5 min)	P	LSD	
Dicots	Mature Chaparral	0.67	1.16	0.90	1.57	1.12	1.11	**	0.40	
	2nd yr Burn	4.76	4.70	4.48	3.55	4.68	3.18	**	0.92	
Monocots ^a	Mature Chaparral	0.23	0.15	0.05	0.17	0.04	0.11	*	0.13	
	2nd yr Burn	10.82	11.25	10.75	10.77	9.08	4.46	**	2.32	

* P < 0.05, ** P < 0.01.
^a All but one of the monocots were grasses.

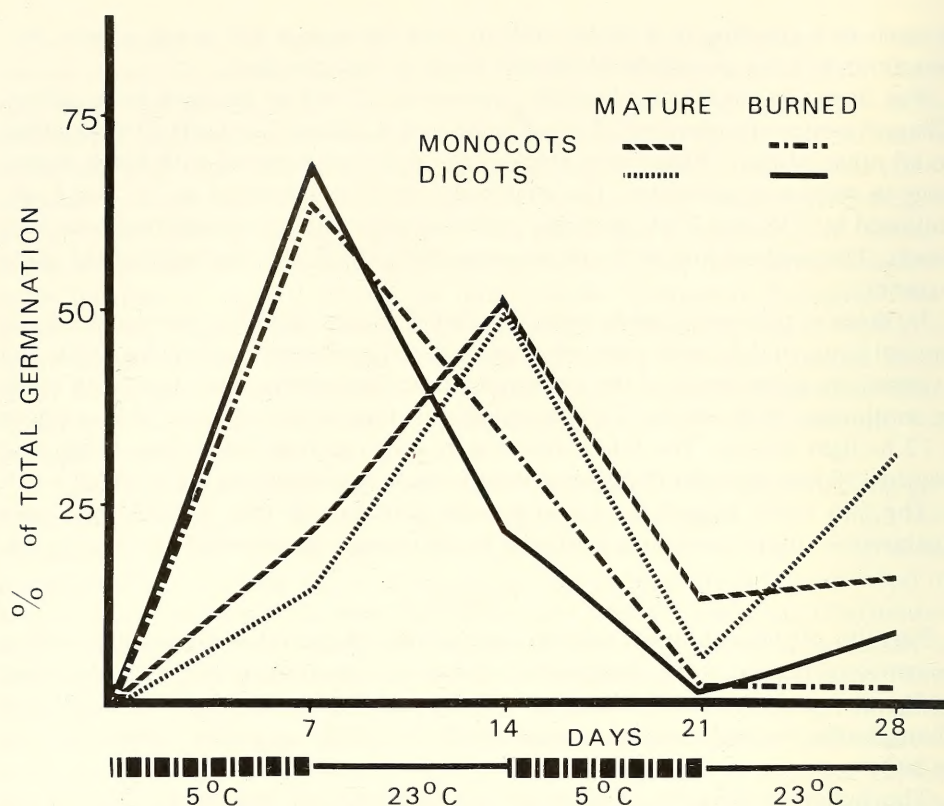


Fig. 1. Rate of germination of monocots and dicots from soils collected from mature chaparral and an adjacent two year burn.

this was not a complication. As will be seen below, germination of *Cryptantha muricata* did not differ on the two soils yet a separate test showed it was sensitive to elevated osmotic pressure; germination was reduced from 77% (S.D. = 12, N = 3) in distilled water controls to 24% (S.D. = 7) in 0.2 M mannitol.

Dicot seedling emergence from mature soils was significantly increased by all treatments, including the supposedly "allelopathic" leachate treatments (Table 1). Charate produced significantly greater germination than any other treatment; sixteen dicot species emerged from these plates: 51% were herbs, largely *Descurainia pinnata*, *Camissonia hirtella*, *Gnaphalium californicum* and the remaining 49% were nearly all *Adenostoma fasciculatum*.

From the second year burn soil, dicot germination was much greater than from the mature chaparral soil and no treatment increased germination over controls. No shrub seedlings emerged from these soils though many of the herb species were the same as those from the mature soil. Addition of charate to this soil significantly reduced germination.

Monocot seeds were rare in mature chaparral soil but abundant in burned chaparral soil. These seeds were essentially all from grasses, largely *Bromus tectorum* and *Festuca megalura*. Heat reduced germination of these grasses in both soils.

Table 2. Percentage germination of species planted into soils after the end of the experiment in Table 1. C.m. and P.c. were sown together and L.s. and S.c. were sown together thus $n = 42$ dishes for each species. Due to the large sample size, seeds were added with a small measuring spoon; mean number of seeds per spoon, $\pm$ S.E. of the mean for $n = 14$, was: 128 ± 6 (C.m.), 92 ± 6 (P.c.), 108 ± 5 (L.s.) and 140 ± 9 (S.c.). Note, for the heat treatment, the soils were heat treated but not the seeds of the four species added.

		Con- trol	4 × Leach- ate	Char- ate	120°C (5 min)	P	LSD
<i>Cryptantha muricata</i>	Mature Chaparral	62	72	78	74	NS	
	2nd yr Burn	64	58	72	63	NS	
<i>Phacelia cicutaria</i>	Mature Chaparral	17	17	26	19	**	6
	2nd yr Burn	20	20	14	18	*	5
<i>Lotus salsuginosus</i>	Mature Chaparral	21	19	21	19	NS	
	2nd yr Burn	**	**	**	**	NS	
<i>Salvia columbariae</i>	Mature Chaparral	9	10	52	9	**	7
	2nd yr Burn	**	**	**	**	NS	

NS $P > 0.05$, * $P < 0.05$, ** $P < 0.01$; $P > 0.05$ for mature vs burn comparisons not starred.

The rate of germination from these soils varied markedly (Fig. 1). For both monocots and dicots germination was much more rapid from the burn soil than from the mature chaparral soil.

After the indigenous seed pool had germinated, these same soil samples were sown with four native herb species (Table 2). There were marked differences in species responses. *Cryptantha muricata* germinated well under control conditions and was not affected by any of the soil treatments. *Phacelia cicutaria* germination was significantly increased with charate on mature soil and decreased with charate on burn soil. Germination of *Lotus salsuginosus* was significantly lower on burn soil regardless of treatment whereas *Salvia columbariae* germination was higher on burn soil unless charate was added to control soil, where germination was high.

The observation that charate enhanced germination in mature chaparral soil but inhibited germination (of some species) in burn soil (Tables 1 and 2) was surprising. In the case of *P. cicutaria* and *S. columbariae* (Table 2) the soils had

Table 3. Seedling emergence from soils incubated in the light (12 hr photoperiod at $\sim 230 \mu\text{E m}^{-2} \text{ s}^{-1}$) and total darkness, with and without charate ($n = 30$).

		Seedlings/50 cc soil					
		Control		Charate			
	Soil	Light	Dark	Light	Dark		
Dicots	Mature Chaparral	1.40	**	0.37	3.80	**	1.70
	2nd yr Burn	6.99	**	3.33	4.87	**	2.80
Monocots	Mature Chaparral	0.13		0.17	0.03		0.03
	2nd yr Burn	10.30	**	7.30	10.67	*	8.53

* $P < 0.05$, ** $P < 0.01$; $P > 0.05$ for light vs dark comparisons not starred.

Table 4. Percentage germination of species sown into soils after the end of the experiment in Table 3 (n = 15).

		Control			Charate		
	Soil	Light		Dark	Light		Dark
<i>Cryptantha muricata</i>	Mature Chaparral	73	**	2	82	**	12
	2nd yr Burn	62	**	10	56	**	9
<i>Phacelia cicutaria</i>	Mature Chaparral	10	**	7	38	**	8
	2nd yr Burn	6		9	3		11
<i>Lotus salsuginosus</i>	Mature Chaparral	18		17	24		21
	2nd yr Burn	14		14	13		15
<i>Salvia columbariae</i>	Mature Chaparral	44	**	1	74	**	33
	2nd yr Burn	84	**	48	59	**	49

* $P < 0.05$, ** $P < 0.01$; $P > 0.05$ for light vs dark comparisons not starred.

been wetted and incubated for a month (to germinate the indigenous seed pool) before sowing. I hypothesized that this long pre-incubation of the soil (and in particular with the addition of charate) allowed growing microbial populations to inhibit germination. I predicted that germination would be much greater if seeds were sown into the burn soil without prior wet incubation of the soil. This was tested with *P. cicutaria* and it was found that burn soils treated as before (with prior incubation) produced 8% (S.D. = 8, N = 15) germination whereas if *P. cicutaria* were sown into burn soil without prior incubation of that soil, germination was 39% (S.D. = 5, N = 15).

Effect of Light

In previous experiments light was not considered; seeds were incubated in the dark although they were exposed to the light when scored. In this experiment germination under a twelve hour photoperiod was compared with germination in total darkness (Table 3). For both mature and burn soils, dicot and monocot seed germination was significantly inhibited by total darkness. The four species sown into these soils illustrate different responses to total darkness (Table 4); *L. salsuginosus* was insensitive to darkness; *C. muricata* and *S. columbariae* were markedly inhibited by total darkness with or without charate; *P. cicutaria* was inhibited by darkness only in the presence of charate.

Apparently the previous experimental conditions of dark incubation followed by scoring in the light approximated the "light stimulating" conditions of the 12

Table 5. Effect of light intensity on germination of seeds from mature chaparral soil and *Cryptantha muricata* planted in the same soil (n = 12). For C.m. seed number is as in Table 2.

	$\mu\text{E m}^{-2} \text{ s}^{-1}$				LSD
	~230	~20	~0	P	
Dicots (NO/50 cc)	1.92	1.92	0.7	**	1.39
Monocots (NO/50 cc)	0.00	0.17	0.17	NS	
<i>Cryptantha muricata</i> (%)	75	57	10	**	16

NS $P > 0.05$, ** $P < 0.01$.

hr photoperiod incubation. This is suggested by a comparison of the charate response in the previous experiments (Tables 1 and 2) with the charate effect under the light treatment (Tables 3 and 4). Although the absolute level of germination was higher under 12 hr photoperiod (Tables 3 and 4) than under periodic light exposure every week (Tables 1 and 2), the relative effect of charate was the same under both conditions. Table 5 shows that the light intensity may be quite low ($\sim 20 \mu\text{E m}^{-2} \text{ s}^{-1}$) and still produce a stimulatory effect on germination.

Discussion and Conclusions

This study does not support the theory that native seeds are inhibited from germinating under the mature chaparral canopy by chemical inhibitors. Indeed so-called "allelopathic" leachate from *Adenostoma* foliage stimulated germination of seeds from the mature chaparral soil. This stimulatory effect has in fact been observed for a variety of species (Keeley et al. 1985) where it has been attributed to the known stimulatory effect of NO_3^- which is abundant in the leachate. Circumstantial evidence of microbial inhibition was observed in the present study but only on burn soil.

Both heat and charred wood produce a highly stimulatory effect on germination of seeds from mature chaparral soil. However, charate stimulated the germination of *Phacelia cicutaria* and *Salvia columbariae* but not *Cryptantha muricata* or *Lotus salsuginosus*.

In comparing the mature chaparral soil and the second year burn soil it is clear that 1) the seed pools are quite different, and 2) the soils affect germination of the same species quite differently. Annual grass seeds were uncommon in the mature chaparral soil whereas they were abundant in the second year burn soil. This suggests that these species invade recently burned areas but their residence time in the soil is low in the absence of fire. Although ignored in previous studies it appears that light plays a major role in the germination of certain chaparral seeds. Certainly the evidence presented here should be sufficient warning that future studies need to examine the effect of light on chaparral seed germination.

Highest germination from mature chaparral soil was with charate under a 12 hr photoperiod. Estimates based on the range of depths soil was sampled suggest this treatment produced ca. $1500 \text{ seedlings/m}^2 \pm 500$. Such numbers are clearly large enough to produce seedling densities typical of burned chaparral stands.

In conclusion it appears from these data that the bulk of the dormant seed pool in mature chaparral requires the stimulating effect of heat, charred wood, and light for germination. Seeds in soil from a 2nd year burned site (still largely devoid of shrub cover) germinated readily without heat or charred wood although a large portion of this seed pool required light for germination.

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Department of Biology, Occidental College, Los Angeles, California 90041.

Appendix I. Soil characteristics for media used in this study compared to commercial (Gro-Lite) potting soil. The mature soil pH in parenthesis is for the soil alone, i.e., without the fine litter (mostly *Adenostoma* leaves).

	Potting soil	Mature chaparral soil	2nd yr burn soil
pH	6.7	5.6 (6.6)	7.3
Na (ppm)	230	75	130
Mg (ppm)	250	21	20
Ca (ppm)	300	200	210
Fe (ppm)	0.6	1.4	1.6
Zn (ppm)	0.2	0.4	0.4
PO ₄ (mg/l)	7.5	0.04	0.60
SO ₄ (mg/l)	96.0	0.00	0.00
NO ₃ (mg/l)	7.9	1.5	0.7
CO ₃ (mg/l)	0.1	0.1	0.6

Seasonal Abundance of Pinnipeds at San Nicolas Island, California, 1980-1982

Brent S. Stewart and Pamela K. Yochem

Abstract. — Seasonal abundance of pinnipeds at San Nicolas Island, California, 1980-1982 by Brent S. Stewart and Pamela K. Yochem. *Bull. Southern California Acad. Sci.*, 83(3):121-132, 1984. Seasonal cycles in abundance of northern elephant seals, California sea lions, harbor seals, and Guadalupe fur seals at San Nicolas Island, California, were monitored by frequent ground and aerial surveys from February 1980 through September 1982. Northern elephant seals were most abundant in late January and early February during the height of their breeding season and again in late April to early May when juveniles and adult females hauled out to molt. Sea lions were most abundant in late June to early July during the height of their breeding season and were least abundant in winter and early spring. Harbor seals were in greatest abundance in late May to early June when they were molting and numbers were lowest in winter. Guadalupe fur seals were present from June through September during their breeding season. Seasonal populations and pup production of elephant seals, sea lions, and harbor seals increased each year.

Three species of pinnipeds, the northern elephant seal (*Mirounga angustirostris*), California sea lion (*Zalophus californianus*) and Pacific harbor seal (*Phoca vitulina richardsi*, Shaughnessy and Fay 1977), breed at San Nicolas Island (SNI), California (33°15'N, 119°30'W). Guadalupe fur seals (*Arctocephalus townsendi*) may have been abundant in the Southern California Bight (SCB) prior to commercial exploitation by sealers in the 19th century (Scammon 1874; Lyon 1937; Walker and Craig 1979), but it is not known if they ever bred at SNI. Steller sea lions (*Eumetopias jubatus*) have been sighted occasionally (Bartholomew 1951; Bartholomew and Boolootian 1960), but they have apparently never bred at SNI. The earliest published data for the SNI sea lion population are from a 1946 census (Ripley et al. 1962) and it has been censused occasionally since then (Bonnot and Ripley 1948; Bartholomew 1951; Bartholomew and Boolootian 1960; Peterson and Bartholomew 1967; Frey and Aplin 1970; Carlisle and Aplin 1971; Odell 1971, 1975a, 1975b; Bonnell et al. 1980). The harbor seal population at SNI has rarely been censused (Bartholomew and Boolootian 1960; Odell 1971; Bonnell et al. 1980). Elephant seals have been censused sporadically since reestablishment of a breeding colony in the early 1950's (Bartholomew 1951; Bartholomew and Boolootian 1960; Odell 1971, 1974, 1977; Bonnell et al. 1980; Antonelis et al. 1981; Cooper and Stewart 1983). The sizes and distributions of populations of each species have changed substantially during the last several years. We report here on the seasonal abundance and distribution of northern elephant seals, California sea lions, harbor seals, and Guadalupe fur seals at SNI from February 1980 through September 1982.

Methods

Forty-three ground and three aerial surveys were made of pinniped breeding and hauling areas at SNI from 3 February 1980 through 1 October 1982. In 1980, we identified census areas by placing permanent wooden markers at the boundaries of each area. These areas and the numerical designations used here (Fig. 1) are in most cases identical to those used by Bonnell et al. (1980) and generally comparable to those that have been used by other authors in the past (Bartholomew 1951; Peterson and Bartholomew 1967; Odell 1974, 1975b, 1977). Ground counts were made on foot using Bushnell 6-18 $\times$ 35 mm zoom binoculars and a Bushnell 20-45 mm zoom spotting scope; seals were classified by species, sex, and age. Aerial surveys were made in a Cessna 337 Skymaster; hauling and breeding areas were photographed obliquely with a Nikon 35 mm camera equipped with a 43-86 mm zoom or 200 mm telephoto lens using Ektachrome (400 ASA) and Fujicolor 400 film. Mounted slides were projected and numbers of animals of each species were counted and classified by age and sex.

Age and sex classification of seals differed for each species. This was necessary because of differences among species in the ease and reliability of consistently identifying large numbers of individuals, often in very dense aggregations, as belonging to specific age and sex categories.

Methods of assessment of pup production (an index of natality; usually the number of pups surviving to some age) and pup mortality also varied among species. We define pup production as the number of live pups that are counted on a particular date; determination of this date is based on knowledge of the breeding biology of each species. We determined pup production for each species by censusing all breeding areas in late February (elephant seals), early April (harbor seals) or early July (California sea lions).

We define pup mortality generally as the number of pups that were observed dead during a specific time period divided by an estimate of the number of pups born during that same time period. Pup mortality was estimated from early December through early March for elephant seals, from late February through late April for harbor seals, and from late May through early July for California sea lions. These estimates are therefore of pre-weaning pup mortality for elephant seals and harbor seals and of whelping season pup mortality for sea lions.

In 1982 we counted essentially all elephant seal pups that died prior to weaning by conducting daily censuses of some rookeries and weekly censuses of all rookeries. In 1980 and 1981 we conducted bi-weekly or monthly censuses of all rookeries. We tied red surveyor's tape around the ankles and necks of most dead pups after we measured and sexed them. To avoid disturbance to females and nursing pups we did not examine a few pups that died in the middle of groups of females. However, we noted the location and state of decomposition of each unmarked carcass on grid maps during each census. Marking and mapping the locations of dead pups prevented double-counting of carcasses.

We recorded all dead harbor seal pups observed from late February through late April. These counts are, necessarily, minimal estimates of mortality for several reasons. Harbor seals can swim at birth (many births are apparently aquatic) and pups move daily between terrestrial hauling areas (beaches, intertidal reefs and ledges) and the sea with their mothers. Pups that die (or are still-born) while ashore

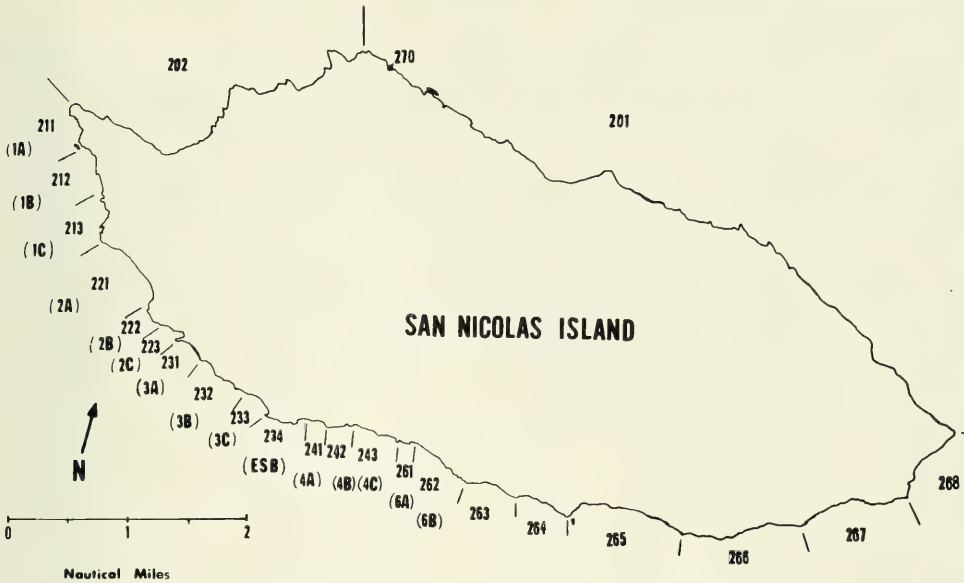


Fig. 1. San Nicolas Island showing census areas and numerical codes.

may therefore not be detected unless the carcasses initially appear well above the high tide line. Pups that die at sea are also unlikely to be detected. Therefore, without specific mark-recapture studies of pups or of parous females, the relationship (and its variability) of observed dead pups to estimates of pup production is unknown.

We estimated sea lion pup mortality by recording the number of new pup carcasses observed on each biweekly census during the whelping season (25 May through 4 July each year). Dead pups found before 25 May were considered to be premature and were not considered as part of the whelping season mortality.

Because most dead sea lion pups could not be marked without major disturbance to rookeries, we simply tallied the number of fresh pup carcasses from observation points above rookeries during biweekly censuses between 25 May and 4 July each year. Sea lion pups are smaller than elephant seal pups and faster rates of decay (both passive and by gull scavenging) and burial in the sand prevented detailed monitoring of the fate of sea lion pup carcasses during the biweekly censuses. We summed counts of dead pups from all censuses during the whelping season to determine a minimal estimate of whelping season mortality. This estimate was derived by dividing the cumulative total of dead pups by an estimate of natality (pup production plus dead pup total).

During the course of other studies, we placed numbered plastic tags (Dalton Jumbo Roto) in the interdigit webbing of the rear flippers of harbor seals and elephant seals at San Nicolas and San Miguel Islands. During the breeding season we also marked adult and subadult male, adult female and newborn elephant seals with bleach and dye, which permitted identification of individuals for several months. Resightings of these tagged and marked animals provided data on seasonal age and sex composition of the populations, which we summarize below.

Results

Northern Elephant Seal.—Adult males began arriving at SNI in late November to early December. The first pregnant females arrived in early to mid-December and some arrived as late as mid-February. The breeding population increased rapidly in January and peak numbers of seals were ashore the last week in January, by which time approximately 85% to 90% of the season's pups had been born (Stewart 1983). Females gave birth approximately 7 days ($\bar{x} = 6.8$, standard error = .05) after coming ashore and remained ashore suckling their pups an average of 27 (standard error = .5) additional days before returning to sea. Some females weaned their pups and departed the rookery as early as 2 January, but most did so during the first two weeks of February (Stewart 1983). All females that gave birth departed the rookery by the first week of March. Females remained at sea for an average of 75 days (standard error = 3.5) before returning to molt, although females that lost pups during the breeding season spent less time at sea ($\bar{x} = 56.3$ days, standard error = 5.21 days) than did females that successfully weaned pups ($\bar{x} = 75.5$ days, standard error = 2.7 days, $t = 3.3$ $P < .01$). Using 15 February as a mean date of departure for females, the adult female molt peak would be expected to occur the first week of May. Our observations of peak numbers of females ashore in late April to early May support this. Some molting females arrived in early March and most had left the island by early June.

Pups were weaned about 27 days (standard error = .5) after birth but remained on the rookery for an additional four to six weeks before going to sea. Weaned pups began leaving the rookery in early March although most departed between mid-March and late April (Table 1). A few were present through late May. A few pups-of-the-year hauled out briefly in September and October and although most had departed by December, a few (now yearlings) remained through January.

The adult and subadult male populations remained fairly constant from early January through late February, although there was some movement of both subadult and adult males between beaches in January. Males began leaving in late February; few were present in mid-March and they were absent from April through early June (Table 1). Subadult males returned to molt in early May and numbers ashore peaked in late May to early June. Numbers of molting adult males increased from June to July peaking in mid-July. Most departed by late August and none were ashore from September through mid-November. Juvenile males and females were absent from the island during the breeding season but numbers ashore increased in late March and early April and peaked in late April when they returned to molt. Most juveniles had returned to sea by late May although a few were present in summer and fall months. Molting seals hauled out almost exclusively at areas 221, 231, 232, and 233 from March through August of each year.

Approximately 1188, 1546, and 2312 pups were born at SNI in 1980, 1981, and 1982 respectively. Annual pup mortality on the island remained fairly constant at 3% to 4%, although beach topography affected pup mortality at specific sites. Highest mortality occurred on narrow, steep-backed beaches when high tides (primarily at peak season in late January) combined with storm-generated surf to wash those beaches, drowning some pups and separating others from their mothers. Numbers of pups born in each area increased during the three-year study (Table 2). Colonization of new beaches on the southern coastline also continued

Table 1. Censuses of northern elephant seals (*Mirounga angustirostris*) at San Nicolas Island, 1980–1982.

Date	Adult males	Sub-adult males	Females	Juveniles	Live pups	Yearlings	Totals
1980							
3 Feb	97	30	1109	2	1075	0	2313
9 Mar	46	2	25	7	884	0	964
21 Apr	0	2	275	965	279	0	1521
17 May	0	54	637	1305	154	0	2150
8 Jun	51	273	146	162	0	0	632
12 Dec	73	32	39	13	1	93	251
27 Dec	106	70	166	39	54	112	547
1981							
10 Jan	106	38	750	1	379	24	1298
23 Jan	130	39	1430	0	1176	4	2779
6 Feb	151	41	1151	0	1401	4	2748
19 Feb	170	24	237	0	1399	0	1831
21 Mar	21	1	19	322	952	0	1315
3 Apr	1	0	198	1944	911	0	3054
*18 Apr	0	12	428	2618	603	0	3661
25 Apr	0	11	692	2310	460	0	3473
8 May	0	149	1458	2004	118	0	3729
*16 May	0	357	1512	1101	0	0	2970
23 May	0	590	1209	504	0	0	2303
12 Jun	0	338	212	18	0	0	568
28 Jun	70	208	0	21	0	0	299
5 Jul	69	188	2	7	0	0	266
11 Jul	96	142	24	12	0	0	274
24 Jul	87	112	1	18	0	0	218
7 Aug	81	37	2	24	9**	0	153
22 Aug	22	20	0	82	13**	0	137
31 Oct	0	8	6	371	218**	0	603
1982							
2 Jan	147	112	468	90	197	10	1024
9 Jan	129	117	849	69	459	8	1631
15 Jan	127	124	1567	23	836	1	2678
22 Jan	151	136	2071	16	1455	0	3829
29 Jan	142	163	2168	19	2064	0	4556
6 Feb	154	100	1747	1	2196	0	4198
12 Feb	126	137	1225	0	2224	0	3712
19 Feb	126	138	506	5	2218	0	2993
26 Feb	106	132	115	7	2238	0	2600
9 Mar	71	50	25	51	1817	0	2014
13 Mar	20	39	68	89	1981	0	2197
10 Apr	0	5	453	1410	1194	0	3062
21 Apr	0	27	473	1943	747	0	3190
11 May	0	130	867	1305	207	0	2509
18 May	0	252	1462	525	36	0	2275
29 May	0	446	639	174	1	0	1259
12 June	9	284	150	253	0	0	696
4 July	131	82	18	78	0	0	309
1 Oct	0	0	184	48	273***	0	505

* Aerial survey; all others are ground counts.

** Pups-of-the-year.

Table 2. Natality and pup mortality of northern elephant seals (*Mirounga angustirostris*) at San Nicolas Island, 1980–1982.

Site	Pups born			Dead pups			% Mortality		
	1980	1981	1982	1980	1981	1982	1980	1981	1982
266	0	14	27	0	3	2	—	21%	7.4%
265	0	61	175	0	1	8	—	1.6%	4.6%
264	29	30	98	0	1	2	0	3.3%	2.0%
261, 262, 263	258	298	361	15	12	7	5.8%	4.0%	1.9%
243	62	30	153	5	0	5	8.1%	0	3.3%
242	39	37	53	1	0	0	2.6%	0	0
234, 241	195	214	232	4	6	7	2.1%	2.8%	3.0%
233	234	406	478	2	10	17	.9%	2.5%	3.6%
232	69	98	217	3	13	5	4.3%	13.3%	2.3%
231	58	87	149	1	2	6	1.7%	2.3%	4.0%
223	96	107	121	9	2	8	9.3%	1.9%	6.6%
221	147	164	246	4	2	7	2.7%	1.2%	2.8%
201	0	0	2	0	0	0	—	—	0
Total	1187	1546	2312	44	52	74	3.7%	3.4%	3.2%

and pups were born on northern shores for the first time in 1982 (Table 2, Fig. 1).

Harbor Seal.—Harbor seals hauled out and gave birth at seven sites and sporadically used 13 others seasonally (Stewart and Yochem 1983). Areas 231 and 266 were the most consistently used hauling areas year-round, although significant numbers were found at area 270 during the whelping and molt seasons. Hauling patterns of harbor seals at most sites on SNI appear to be similar to those of harbor seals at San Miguel Island (Stewart 1981a, 1984; Stewart and Yochem 1983), with peak numbers hauled out in early afternoon.

Few harbor seals were ashore from September through February. Numbers began to increase in late February when females began giving birth. Pups were born from late February through late April and pups were most abundant in early April. In 1982 one premature pup, still in lanugo, was observed on 9 February. Most pups were weaned by mid-May. At least 26 pups were born in 1980 and at least 65 and 85 pups were born in 1981 and 1982, respectively.

The number of seals ashore increased through spring; maximum numbers were present in late May to early June (Table 3). This peak in abundance was related to the annual molt; some seals began shedding in early May and most had completed the molt by late July. Numbers ashore declined steadily from late June through December (Table 3). Live pups represented approximately 14% of the whelping season population in 1980, 28% in 1981, and 24% in 1982; but 10%, 11%, and 12% of peak (late May) populations in 1980, 1981, and 1982 respectively.

Based on the maximum number of pups observed and the total number of pup carcasses encountered, minimal pup mortality estimates were 7% in 1980, 12% in 1981, and 7% in 1982. Of eight dead pups found in 1981, six were found at sites where disturbance by humans is frequent. Disturbance at beaches when young harbor seal pups are present often causes separation of mothers and pups and

Table 3. Censuses of harbor seals (*Phoca vitulina richardsi*) at San Nicolas Island, California, 1980–1982.

Date	Pups	Total	Date	Pups	Total
1980			1982		
3 Feb		62	2 Jan		81
9 Mar	3	45	15 Jan		46
21 Apr	26	207	22 Jan		80
4 May	5	226	29 Jan		37
17 May	9	257	6 Feb	1	131
8 Jun		312	12 Feb		76
6 Jul		283	19 Feb		41
12 Dec		17	26 Feb		44
27 Dec		29	9 Mar	9	82
1981			13 Mar	38	346
10 Jan		7	3 Apr	84	304
23 Jan		211	21 Apr	48	229
6 Feb		39	11 May	39	605
19 Feb		122	18 May	26	609
21 Mar	47	184	29 May	7	566
3 Apr	63	227	2 June	13	694
*18 Apr	20	242	12 June	7	661
25 Apr	65	296	4 July	4	399
8 May	38	371			
*16 May	59	566			
23 May	40	530			
12 Jun	13	452			
*29 Jun	31	444			
5 Jul	25	350			
11 Jul	62	333			
24 Jul	28	177			
7 Aug	3	121			
22 Aug	3	192			
10 Oct		194			

* Aerial survey; all others are ground counts.

subsequent starvation and death of pups (Pitcher and Calkins 1979; Johnson 1977; Stewart and Yochem, pers. obs.).

California Sea Lion.—The California sea lion population peaked in early July coincident with the height of the breeding season. The July peak increased 14% from 1980 to 1981, and 24% from 1981 to 1982 (Table 4).

Births occurred from late May through early July. The greatest number of births occurred in mid-June. Premature pups (6 in 1980, 7 in 1981, 16 in 1982) were observed from January through mid-May. Pup production was approximately 6096 in 1980, 6704 in 1981, and 7738 in 1982 (Table 5). During the whelping season 186 dead pups were observed in 1980, 113 dead pups were observed in 1981, and 123 dead pups were observed in 1982. Minimal mortality during the whelping season at specific breeding sites ranged from 1.4% to 20% in 1980, 2.1% to 12.5% in 1981, and 1.0% to 4.9% in 1982. Absolute pup mortality is presumably somewhat greater but its measurement is complex. Detection of dead sea lion pups is influenced by weather and tide conditions, beach topography, variable

Table 4. Censuses of California sea lions (*Zalophus californianus*) at San Nicolas Island, California, 1980-1982.

Date	Males	Subadult males/ females/juveniles		Live pups	Total
1980					
3 Feb	186		4649	0	4835
9 Mar	195		5822	0	6017
19 Apr	149		6260	4	6413
17 May	140		4096	34	4271
8 Jun	360		5205	1276	6841
6 Jul	284		7927	6096	14,307
12 Dec	232		3545	—	3777
27 Dec	60		3615	—	3675
1981					
10 Jan	62		3576	—	3638
23 Jan	75		3404	—	3479
6 Feb	74		3721	—	3795
19 Feb	148		4650	—	4798
21 Mar	119		5029	—	5148
3 Apr	201		6460	2	6663
*18 Apr	248		7703	0	7951
25 Apr	216		9244	5	9465
8 May	187		5572	0	5759
*16 May	153		5224	0	5377
22 May	157		5015	121	5293
12 Jun	925		10,204	3336	14,465
5 Jul	637		8668	6704	16,006
11 Jul	1437		8290	6626	16,353
24 Jul	458		7541	6676	14,654
7 Aug	33		4275	6370	10,678
22 Aug	19		5246	4851	10,116
		Subadult males	Females/ juveniles		
1982					
2 Jan	25	100	3990	—	4115
9 Jan	29	182	3573	—	3784
15 Jan	43	209	6728	—	6980
22 Jan	43	285	5033	—	5361
29 Jan	62	196	4839	—	5097
6 Feb	69	276	3315	—	3660
12 Feb	122	342	5473	—	5937
19 Feb	131	280	5655	—	6066
26 Feb	105	577	6696	—	7378
9 Mar	70	431	6365	—	6966
13 Mar	43	407	6757	—	7207
10 Apr	35	245	6610	—	6890
11 May	43	231	4124	—	4424
18 May	42	205	3839	—	4109
29 May	90	194	5793	274	6381
12 June	261		10,845	3396	14,502
4 July	519		12,035	7738	20,292
1 Oct	0	43	3296	3790	7129

* Aerial survey; all others are ground counts.

Table 5. Pup production of California sea lions at specific sites at San Nicolas Island, 1980–1982.

Site	Pup production		
	1980	1981	1982
266	0	0	0
264	0	0	0
263	0	0	0
262	483	527	474
261	281	293	355
243	859	864	1030
242	501	560	786
241	795	867	358
234	359	368	366
233	1078	1140	1422
232	469	503	1207
231	351	387	497
223	465	533	806
221	72	101	53
213	12	22	25
212	182	254	164
211	189	285	195
Total	6096	6704	7738

rates of carcass decomposition and disappearance, and frequency of censuses (Heath and Francis 1983; Stewart and Yochem, unpubl. data).

The number of adult males ashore fluctuated at low levels throughout the winter. Breeding males first arrived and established territories in mid-May. The male population then increased rapidly in June and peaked in early July during the height of the breeding season. The adult male population declined rapidly in late July as territories disintegrated and males returned to sea; few were present in August and September (Table 4). Subadult males increased in number briefly in February and March and then declined before increasing again in late May.

Adult females and juveniles of both sexes were included in a single census category ('others'); their numbers were lowest in January and February, peaked briefly in April and then declined through late May. Numbers then increased sharply to a peak in mid-late June, corresponding to a peak in whelping activity.

The number of sea lions declined from October through December, during which time the population was composed primarily of pups-of-the-year, attending females and, to a lesser extent, juveniles. Most areas used by breeding sea lions were also used as hauling areas during the non-breeding season. The east end of 221 was used exclusively by bachelor and subadult males during the breeding season. Although a few pups were born at the west end of 221, this area was not used by sea lions during the non-breeding season. Relatively few sea lions used the rocky shoreline in areas 211, 212, and 213 for hauling during the non-breeding season. During the breeding season, most juveniles and non-breeding females aggregated on beaches in areas 231, 241, and 262. Large numbers of pups were, however, born on reefs and bluffs at the west ends of areas 262 and 233. Area 241 was used considerably less for pupping in 1982 than in the previous two years. The reasons for this are unclear but repeated human disturbance of hauled

seals (resulting in relocation of some seals to other sites) may be among them. Although pup production increased 25% from 1980 to 1982 the relative proportion of pups born in each area remained fairly constant. In 1982 approximately 34% of all pups were born within a $\frac{1}{2}$ to $\frac{3}{4}$ km stretch of coastline in areas 232 and 233. Areas 223, 242, and 243 were other major whelping areas (Table 5).

Guadalupe Fur Seal.—An adult male Guadalupe fur seal maintained a territory in area 242 from about 26 June through 2 August 1981; a juvenile fur seal was seen in the same area on 4 July 1981 but was not seen again (Stewart 1981b).

In 1982 the same adult male (identified by scars) maintained a territory in the same location from at least 26 May through 1 October. Lone immature seals were observed at other sites (232, 223) in July 1982 (P. Yochem, unpubl. data; J. Francis and C. Heath, pers. comm.). We also saw an immature fur seal within 100 meters of the adult male on 1 October 1982.

Discussion

Elephant seals were first reported at San Nicolas Island in 1949 (Bartholomew 1951) and although published records of pups do not appear until 1959 (Bartholomew and Boolootian 1960) pups may have been born there as early as 1951 (Odell 1974). The initial breeding population was apparently restricted to areas 232 and 233. Pup production increased from 1959 through 1982 at an average rate of about 16% per year (Cooper and Stewart 1983). Coincident with the population growth has been continued expansion of breeding to new areas along the south side of SNI; in 1981 pups were born from area 221 eastward into the western portion of 266. In 1982 pups were born even farther east in area 266 and two pups were born on the island's north side in area 201. We assume that food availability is not presently a limiting factor to population growth and we expect the SNI population to increase until beaches become saturated and growth is stabilized by density dependent influences on female breeding success and pup survival. Adequate beach space is available in areas 266 to 268; increased use of some northern beaches may also occur depending on the effects of weather on breeding success there.

Few historical data are available on the harbor seal population at SNI. Bartholomew (1951) reported 141 and 177 seals on 18–20 June 1949 and 9–11 July 1949, respectively. Bartholomew and Boolootian (1960) reported 21 harbor seals on 16 April 1958 and 34 on 9 June 1958. Bartholomew (1967) believed the population of harbor seals at the Southern California Channel Islands in 1965 to be about 500. Odell (1971) estimated the minimum Channel Islands population at 645 in June 1964; on 20 June 1964, 95 harbor seals were counted at SNI. Bonnell et al. (1980) surveyed the Southern California Channel Islands from 1975 to 1978; the greatest number of harbor seals observed at SNI was 311 in late May 1977. The largest number of pups observed by these authors was 29 in March of 1977. The peak 1982 population count reported here (694) is the largest yet reported for San Nicolas, suggesting the population is increasing. The consistent increase in number of pups observed from 1980 through 1982 also suggests that the population is increasing.

The first data on sea lion pup production at SNI were presented by Bartholomew (1951); all 895 pups seen in 1949 were in areas 211 to 213. Subsequent pup counts reported by Peterson and Bartholomew (1967) and Bartholomew (1967) indicated

that approximately 62% (2244) of the pups born in 1965 were found in areas 211–213. Since then there has been a drastic decline in use of these areas for whelping, presumably due to repeated human disturbance. Bonnell et al. (1980) reported that 55 and 73 pups were born in areas 211 to 213 in 1975 and 1976 respectively; no pups were observed there in 1977. The Point Mugu Naval Air Station and SNI Commands subsequently closed these areas to non-authorized personnel during the whelping and breeding season. By 1980 sea lions had recolonized these areas and at least 400 pups were born there that year. A continued increase in pup production is expected if human disturbance is minimized.

Although data on the Guadalupe fur seal population at Isla de Guadalupe, Mexico, are few, they indicate a slow recovery from nineteenth century overharvesting (Peterson et al. 1968; Fleischer 1978). Increased frequency of sightings of young and mature animals on the Southern California Channel Islands (Bartholomew 1950; Antonelis and Fiscus 1980; Stewart 1981b and this report; DeLong 1982) in recent years seem indicative of a growing population on the species' sole rookery at Isla de Guadalupe. The health and trends in growth of that population will likely be the major factors influencing successful (re)establishment of a breeding colony on the Southern California Channel Islands in the near future.

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Hubbs-Sea World Research Institute, 1700 South Shores Road, San Diego, California 92109.

The Use of Jackknife Confidence Intervals with the Richards Curve for Describing Avian Growth Patterns

David W. Bradley,¹ Ross E. Landry,² and Charles T. Collins²

Abstract.—The use of jackknife confidence intervals with the Richards Curve for describing avian growth patterns by David W. Bradley, Ross E. Landry, and Charles T. Collins. *Bull. Southern California Acad. Sci.*, 83(3):133–147, 1984. A method is presented for measuring growth patterns in birds in which the Richards curve is used as a smoothing device for extracting convenient summary statistics from raw growth data. Jackknife confidence intervals for these statistics are developed and evaluated with Monte Carlo simulation. Strategies for making interspecific and intraspecific comparisons among populations are discussed for both longitudinal and cross-sectional sampling schemes with emphasis on the appropriate scope of inference from different levels of sampling.

Growth patterns have been a focal point in studies of avian reproduction (Ricklefs 1968a, 1973, 1974). However, difficulties arise in such analyses because the pattern of growth for any individual organism is the result of a continuous process of change through time which is observed at a finite number of points. Dependencies among these data complicate the process of estimation and inference. One method which has been widely used in avian studies was developed by Ricklefs (1967) and employs graphical techniques to fit three common growth curves. A more general approach (requiring an iterative curve fitting algorithm) adds flexibility by making use of Richards' (1959) growth function.

Sandland and McGilchrist (1979) reviewed past work and described desirable features for models of growth data. They emphasized differences between linear, nonlinear, deterministic, and stochastic statistical models. Following Ricklefs (1983), we stress the importance of levels sampling in determining the scope of inference within longitudinal, mixed longitudinal, and cross-sectional sampling designs. Our primary concern is development of techniques applicable with cross-sectional data for comparing growth patterns among populations.

Our analysis techniques are illustrated with two sets of data which use body weight as the size criterion. The first dataset contains 2002 measurements from 76 banded, nestling Burrowing Owls (*Athene cunicularia*) of known age. These data were recorded during 1974 and 1975 at Seal Beach Naval Weapons Station, Orange County, California (Landry 1979). They form a longitudinal sample which can be used to compare methods designed for longitudinal data with those appropriate for cross-sectional sampling schemes. The second data set includes 423 weighings of Least Terns (*Sterna antillarum*). Some terns were measured more than once, but the separation between successive measurements, about one week, was long enough so that the data could safely be treated as strictly cross-sectional throughout this study. The terns were captured and banded between 1979 and 1981 in three coastal nesting sites in Los Angeles and Orange counties, California (Collins and Atwood, unpublished data).

$$W = A(1 + (M - 1)e^{-K(T-I)})^{\frac{1}{(1-M)}} \quad 1)$$

Where:

- T = the time of measurement (age of the organism)
- W = the size of the organism at time T
- A = the asymptotic size after growth is completed
- K = a growth constant (controlling the rate of growth)
- I = the time to reach the inflection point in the curve
- M = a shape constant (controlling the shape of the curve).

This differs slightly from Richard's original parameterization of the curve by expressing the multiplier for the exponential term as the time to reach the inflection point in the curve. It also has the advantage that the ambiguity of sign in the exponential term is removed while the other parameters are left unchanged in a manner generally comparable to but not quite identical to that proposed by Fletcher (1975). A derivation of our parameterization from Richards' original formulation is presented in the appendix.

Four parameters are used to fit Richards' curve although only three are of importance in describing the growth pattern. The time scale parameter (I) merely positions the curve along the x-axis, and is not directly comparable for separate curves since it depends upon the values for K and M. An alternative fitting strategy which is more appropriate in the context of stochastic models eliminates the need for this fourth parameter by setting the starting weight as a fixed initial condition (Fletcher 1975; White and Brisbin 1980). That approach simplifies the fitting process by reducing the number of parameters but has the disadvantage (for our purposes) that the curve is forced to pass exactly through the first data point. We choose to retain the time scale parameter (I) thus giving the initial data point equal standing with the rest of the points.

The parameters lead to convenient summary statistics describing the general growth pattern. We follow Richards (1959) in selecting asymptotic size (A), weighted mean growth rate (R), and percentage of asymptotic size achieved at inflection (P) as effective statistics. We also include the time to pass from ten percent to ninety percent of asymptotic size (G) since it has been used in prior studies (Ricklefs 1967, 1968a, 1973; Ricklefs and White 1981) as an indicator of the duration of the primary growth period. These statistics are defined as follows:

A = the raw parameter value from the curve

$$R = \frac{K}{M} \quad 2)$$

$$P = M^{\frac{1}{(1-M)}} \quad 3)$$

$$G = \ln((1 - .10^{1-M})/(1 - .90^{1-M}))/K. \quad 4)$$

Figure 2 illustrates how these summary statistics arise from the growth curve. The time to reach the inflection point (I) merely sets the time scale and conse-

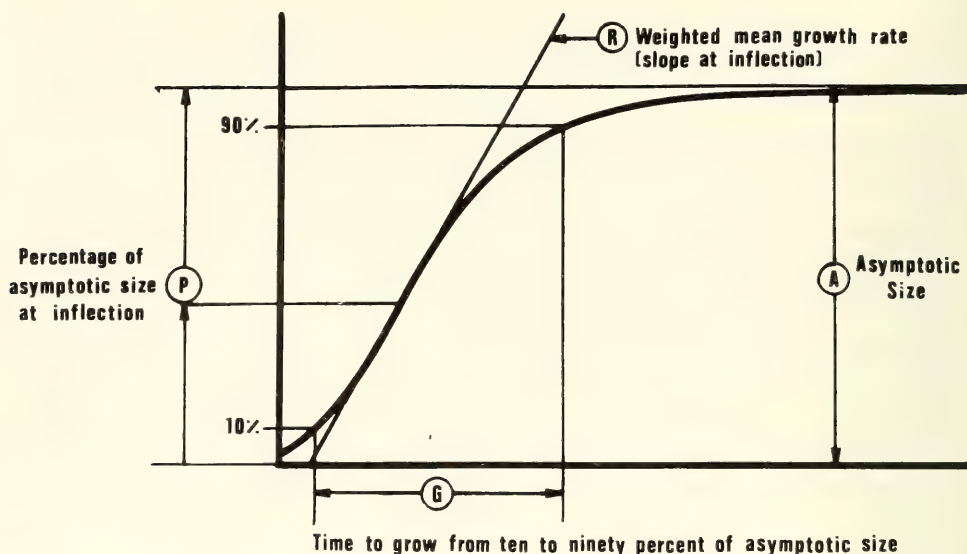


Fig. 2. Graphical representation of summary statistics from growth parameters. Note that the weighted mean growth rate corresponds to the slope at inflection only when the scale of the ordinate is set so that the inflection point occurs at 1.0.

quently is not reflected in the summary statistics. The formula for G is derived in the appendix.

The formulas for Richards' curve degenerate when the shape parameter (M) reaches exactly one. However, the curve asymptotically approaches the Gompertz curve as M approaches 1. Thus the following formulas for the Gompertz curve replace the above equations in this limiting case:

$$W = Ae^{-e^{-K(T-1)}} \quad 1a)$$

$$P = 1/e = 0.36788 \quad 3a)$$

$$G = \ln(\ln(.10)/\ln(.90))/K = 3.0844/K. \quad 4a)$$

The curve can be fitted to raw data with careful application of nonlinear regression methodology. Davies and Ku (1977) point out that Richards' curve is difficult to fit because it tends to produce a long narrow valley in the response surface. In particular, they demonstrated that Causton's (1969) Newton-Raphson approach fails. We used a modified Gauss-Newton algorithm which resembles Marquardt's (1963) method in its use of ridge regression steps to recover from singularities but differs because pure Gauss-Newton steps are taken whenever possible. Thus in our method, the ridge parameter remains at zero until singularities arise.

Since variability in size is often essentially proportional to overall size, we employ a log transformation of the size measures when fitting the curve. This equalizes the variance of the residuals across time and substantially improves the curve fit at early ages over results obtained with raw residuals.

The fact that the Richards' curve is specified by four parameters does not imply that four independent aspects of the growth pattern are being quantified. These

Table 1. Correlations among parameters and summary statistics.

Raw parameters					Summary statistics			
A	1.00							
K	-.57	1.00						
I	.16	.26	1.00					
M	-.50	.95	.52	1.00				
A	1.00	-.56	.16	-.50	1.00			
R	-.26	.08	-.80	-.18	-.26	1.00		
P	-.47	.89	.54	.95	-.47	-.27	1.00	
G	.52	-.65	.07	-.56	.52	-.31	-.68	1.00
	A	K	I	M	A	R	P	G

parameters have substantial interaction in the fitting process, most notable being parallel adjustments of K and M which can result in very similar curves. The summary statistics themselves are interdependent as well.

Table 1 illustrates this effect for the complete set of Burrowing Owl data. There are very high correlations among the raw parameters and moderately high correlations among the final transformed summary statistics. The strong correlations between the raw parameters and the summary statistics are, of course, induced by the definition of the summary statistics.

Confidence Intervals for Summary Statistics

In addition to providing measures which summarize growth patterns, it is desirable to have some indication of the accuracy of these measurements. We explore three ways of achieving this by computing confidence intervals for the summary statistics. One approach fits separate curves to each individual bird in the sample and then uses the ordinary confidence interval around the mean for each summary statistic. A second method, widely used in nonlinear regression, builds a confidence interval for function parameters from the asymptotic variance of their estimates (Venus and Causton 1979). A third method, which we discuss in detail in this section, is the Jackknife, developed by Quenouille (1956) and Mosteller and Tukey (1977).

The jackknife simulates the sampling distribution of the targeted summary statistic by estimating how the value might have changed if a different sample had been drawn. This is done by repeatedly calculating the statistic on different subsamples of the data, where each subsample includes all but one of the original cases. These resampled estimates are then converted by the jackknife transform into pseudo values which approximate the sampling distribution of the statistic:

$$V_i = N * U - (N - 1) * U_{-i} \quad (5)$$

Where:

- V_i = The statistic's pseudo value for the i th individual
- U = Parameter estimate for the whole population
- U_{-i} = The parameter estimate excluding the i th individual
- N = The number of individuals in the sample.

Previous studies of the effectiveness of the jackknife in nonlinear regression had reasonable success in obtaining univariate confidence intervals tempered by poor performance in the multivariate case (Duncan 1978; Fox, Hinkley, and Larntz 1980). They computed separate regressions omitting one case at a time and transformed the resulting parameter estimates with the jackknife formula. Approximate ninety-five percent confidence intervals were then obtained from the mean (m) and standard error (s) of the pseudo values:

$$CI = m \pm s(t_{.025, N-1}) \quad 6)$$

where N is the number of independent pseudo values (cases).

We computed pseudo values for three of the summary statistics (A , R , G) after conversion from the raw parameters (A , K , I , M). A logarithmic transformation prior to applying the jackknife transform gave them a reasonably symmetric distribution. Thus logarithms of A , R , G , and M were substituted for U in equation 5 instead of the raw values. Confidence intervals were obtained by inserting logarithmic scale values into equation 6 and then converting back to the original scale by taking anti-logarithms. Values for M were further transformed with equation 3 into percentage of asymptotic size.

Fortunately, it is not really necessary to perform separate nonlinear fits with each case deleted. The pseudo values can be accurately approximated with linear regression near the estimate obtained for the entire sample (Fox et al. 1980). This is achieved by approximating the nonlinear response surface by a linear manifold near the optimal solution point. We verified that this method performs well for the growth curve application using a subset of the Burrowing Owl data. Correlations between true least squares estimates and the linear approximations ranged from .998 to .999 for the four parameters and none of the linear estimates differed by more than one percent from their corresponding true values.

The entire set of data for each individual should be considered as a single case for resampling. Thus with mixed or longitudinal data omission of a single case involves deletion of more than one data point whenever multiple points are taken for one case. Pseudo values are then obtained for each case rather than each separate data point. This assures that the obtained pseudo values are independent, and avoids overstating the degrees of freedom present in the data.

A Monte Carlo experiment was used to assess the accuracy of the estimates and the confidence interval coverage rates. The idea was to sample individuals from known populations and then compare the sample-based point estimates and confidence intervals to the known population values. Bias, relative efficiency, and confidence interval coverage rates were used to compare the effectiveness of estimates based upon the mean pseudo value with those centered at the summary statistics directly obtained from the curves.

Ideally, this would be done with infinite populations. In order to obtain realistic growth data, we used the actual data on owls and terns (described earlier), with the hope that this restriction to finite populations would not seriously bias the results. Figure 3 reports the results for six trials (each based upon 500 random samples) with varying sample sizes. All of the Monte Carlo work done in this project was accomplished with programs written in APL using the internal random number generator (Roll: "?") with APLUM 2.1 on a Control Data Corporation Cyber 174 computer.

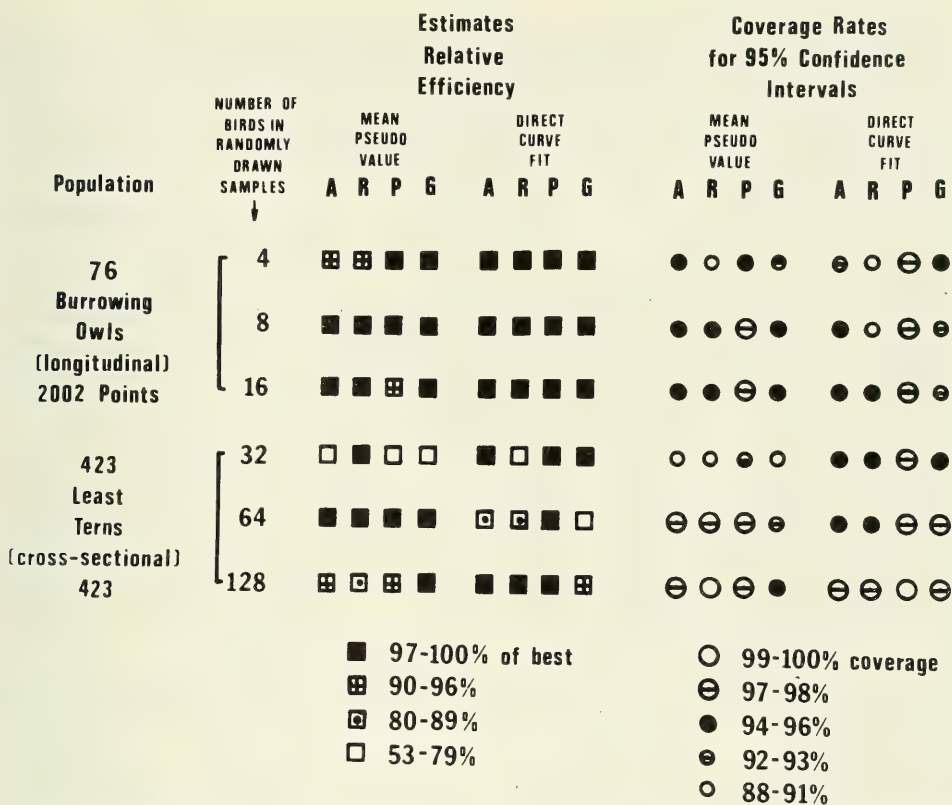


Fig. 3. Relative efficiency of estimators and confidence interval coverage rates. The direct fit refers to estimates obtained directly from the least squares curve parameters and the corresponding confidence intervals centered about these estimates. The other estimates (and confidence intervals) were based upon the mean of the pseudo values from the jackknife.

There are two common reasons for application of the jackknife: 1) confidence interval estimation, and 2) bias reduction. Our simulations were designed to assess its value in the growth curve application for each of these purposes. The results indicated that bias in the estimates of the summary statistics should be of little concern since the squared bias averaged only three percent of the mean squared error in these estimates. Furthermore, Figure 3 shows that the direct estimates performed slightly better than those based upon the mean of pseudo values with respect to both relative efficiency and confidence interval coverage rates. We conclude that the primary value of the jackknife in this situation is for confidence interval estimation and that estimates of the summary statistics should be computed directly from the curve parameters. The coverage rates displayed in Figure 3 are sufficiently close to the nominal level to recommend the use of jackknife confidence intervals in this application.

Scope of Inference

The three methods described above for building confidence intervals around the summary statistics vary in the scope of inference which they support. Intervals

obtained as standard confidence intervals for the mean from separate fits of curves to each individual allow direct inference to the population from which these individuals were sampled (Fig. 1). Ordinary statistical analysis techniques for comparing populations, such as multivariate analysis of variance are also applicable in this situation. In particular, nested designs may be appropriate when several broods are measured for each population.

In contrast, use of the asymptotic covariance matrix as the basis for confidence intervals yields a more narrow scope for inference. This approach would provide confidence intervals for the parameter values for each bird individually if separate curves were fitted per bird. This corresponds to the third level of sampling (Fig. 1) where data points are selected for a single individual. It indicates how the results might have changed if different time points had been measured for the same birds. These intervals could give tests for differences in parameters between selected birds. This approach also provides a basis for computing confidence intervals for a bird's weight at any point in time (Venus and Causton 1979).

If cross-sectional sampling was employed, these intervals could provide tests for differences between populations, since in that case deviations from a curve correspond to random variation among individuals in the population. However, the asymptotic variance approach would not be appropriate for mixed longitudinal sampling schemes since the independence of residuals would not be satisfied and the degrees of freedom would be overstated (Ricklefs 1983).

Fortunately, the jackknife confidence intervals (when built by treating all points measured on any single individual as a single case) are appropriate for inference about populations even when used with mixed sampling schemes. They have the additional advantage that (unlike asymptotic variance intervals) they can easily be obtained for summary statistics which are nonlinear transformations of more than one original parameter (e.g., G obtained from K and M).

When these jackknife confidence intervals are used with longitudinal sampling, they provide estimates of the accuracy of fit for a single curve through all of the data for a sample. This would permit comparison to other similar intervals obtained with cross-sectional or mixed sampling schemes. Intervals obtained from separate fits to each individual in the longitudinal design would not be comparable to these jackknife intervals, since they estimate a different population parameter.

Table 2 shows the parameter estimates and confidence interval widths obtained by all three methods for asymptotic weight with the complete set of 78 Burrowing Owls, and also for a selected subset of six owls. The estimates for the asymptotic and jackknife approaches are of course identical, and differ from the separate curve estimate. The asymptotic theory intervals are narrower than the others. However, they cannot be used as interval estimates of the asymptotic weight for the population of Burrowing Owls from which this sample was taken. Instead, the asymptotic theory intervals properly only estimate how the asymptote for these particular owls might vary had they been measured at different time points. Since the former scope of inference (to population parameters) is of more general interest, the separate curve or jackknife intervals would usually be preferred to the asymptotic theory intervals. The difference is most pronounced with the smaller sample.

In contrast, when the jackknife (width 3.6) and asymptotic (width 4.3) confidence intervals are compared for the complete data set on Least Terns, there is

Table 2. Estimates and confidence interval widths for asymptotic weight.

	All 78 owls		Subset of 6 owls	
	Asymptote	Width	Asymptote	Width
Asymptotic theory	140	(3.7)	134	(17)
Jackknife	140	(6.6)	134	(40)
Separate fit	143	(6.2)	138	(53)

much less difference in the results. This reflects the fact that both approaches have the same scope of inference (to population parameters) with cross-sectional sampling. They differ only in the form of approximation used to build the intervals.

Comparison of Sampling Strategies

Many factors influence the choice of sampling scheme. Often non-statistical considerations take priority. For example, if subjects must be sacrificed in order to make the measurements, only cross sectional data can be obtained (Brisbin and Tally 1973). In field studies, gathering longitudinal data requires frequent handling and possible disturbance of the subjects. This may not be acceptable with some species, necessitating restricted visitation and limited collection of data per individual. In contrast, the difficulty of making repeated measurements in laboratory work is often minor compared with the cost of preparation for the total experimental setting. In such situations observers normally collect longitudinal data.

Statistical considerations generally favor longitudinal sampling schemes. A wide variety of analytical techniques may be used to explore longitudinal data once they have been transformed into summary statistics. Longitudinal designs have one additional advantage. Since the summary statistics do not depend upon the time scale parameter (I), they can be calculated even if the exact age of a subject is unknown. The main disadvantage is the difficulty of data collection, particularly under field conditions.

Proper choice of sampling design also depends upon the relative power of different strategies. Is it better to add more cases or more points per case? We performed a Monte Carlo simulation to answer this question. This experiment involved only the Burrowing Owl data and was designed to assess the relationships among 1) the power of the sampling design (as expressed by confidence interval width), 2) the number of points per bird, and 3) the number of birds measured. Each trial proceeded with a two stage sampling scheme. First n (ranging from 2 to 32) owls were randomly selected from the 78 available. Then p (from 2 to 16) points were chosen from each bird's data. Median confidence interval widths based upon 100 trials per cell appear in Table 3.

The results confirm our *a priori* expectation that it is better to sacrifice points per case (if necessary) in order to measure as many individuals as possible. One potential exception to this recommendation is the case where sufficient points may be obtained per case to treat the data as a longitudinal data set. Here the advantages of longitudinal designs may outweigh the loss of power which accompanied reduction in sample size. In any case, a reasonable number of data must be obtained if any generalizations are to be drawn from the sample. Overall, the

Table 3. Confidence interval widths based upon 100 trials for each cell with the Burrowing Owl data.

Number of cases	Number of points per case			
	2	4	8	16
2	—	—	.93	.90
4	—	.73	.51	.26
8	.63	.34	.21	.14
16	.34	.22	.13	.09
32	.21	.13	.09	.06

Cells in the upper left corner included too few total data points and consequently were omitted.

intervals in Table 3 were reasonably narrow only when at least eight cases and 128 total data points were included.

Example

To illustrate how these techniques work with actual data, we arbitrarily selected a pair of broods of Burrowing Owls for presentation as an example of comparison between groups. Since the owl data are longitudinal in format, it was possible to run the standard analysis obtained by fitting separate curves to each individual. Thus confidence intervals for the mean of each summary statistic were computed using the traditional technique based upon the *t*-distribution (Sokal and Rohlf 1969). In addition, jackknife confidence intervals were developed for summary statistics based upon fitting a single curve through each brood's data.

In addition to the confidence intervals, we computed comparison intervals which were inspired by the work of Gabriel (1978), and in this application cover exactly half of the range covered by the confidence intervals. The intent is simplification of comparison between groups, with significant differences occurring whenever comparison intervals fail to overlap each other. When several samples are to be compared, the overall experimentwise error rate could be controlled by adapting multiple comparison techniques. For example, the Bonferroni inequality could be used (Green 1978). The method of Gabriel (1978) or the more recent refinements by Andrews, Snee, and Sarner (1980) or Hochberg, Weiss, and Hart (1982) provide alternatives.

The resulting confidence and comparison intervals are plotted in Figure 4. Here the first brood grew more quickly than the second since it had a higher weighted mean relative growth rate (*R*) and a shorter growth period (*G*). This brood also reached the inflection point at a higher percentage of asymptotic weight (*P*). However, it stabilized at a lower asymptote (*A*) than the second brood. These patterns are essentially the same with both methods of computing confidence intervals. In fact, the relative widths and positions of these intervals are quite similar for the two methods. The main difference is that, for this example, the estimates are lower when a single curve is fitted through pooled data than those obtained as means from separate fits. This is not surprising, since the two methods estimate different population parameters.

The brood that had a higher weight at inflection was the one which grew most rapidly. This seems reasonable, since a larger proportion of its growth period

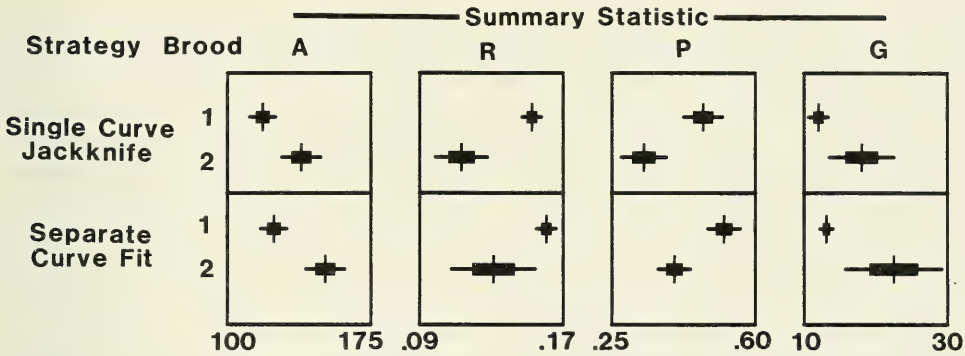


Fig. 4. Comparison of the summary statistics for two arbitrarily selected broods of Burrowing Owls. The upper panel shows results from fitting a single curve to each brood's data and then using the jackknife to compute confidence intervals. The lower panel fits separate curves for each bird and uses the ordinary confidence intervals for a mean (based upon the t-statistic). The plot symbols identify the estimate with a vertical bar. Comparison intervals correspond to the broad horizontal bars, while the narrower horizontal bars mark the confidence intervals. The four summary statistics are asymptotic size (A), weighted mean growth rate (R), percentage of asymptotic size at inflection (P), time to pass from 10% to 90% of asymptotic size (G).

occurred in the exponential gain phase. This brood also reached a lower asymptote, perhaps resulting from its restricted growth period. These observations reflect the fact that the four summary statistics are highly interdependent.

If the two groups of birds being compared here had been randomly sampled from two different populations, or randomly assigned two different treatments, then the proper scope of inference in this analysis would be to differences between populations or treatments based upon the second level of sampling presented in Figure 1. In reality, the data incorporate two entire broods, with the individuals completely enumerated rather than randomly sampled. Thus in this case the scope of inference is to differences between broods based upon the third level of sampling (Fig. 1). Here shorter confidence intervals could likely have been obtained by jackknifing individual data points rather than entire birds, although the observed differences were so substantial that this extra power was not needed in order to detect differences between the groups.

Discussion

Problems in application of the Richards curve may arise from three sources: 1) autocorrelation among the residuals from the curve, 2) intercorrelation among the parameters for the curve, and 3) truncation of the data prior to stabilization at the asymptote. Each will be considered in turn.

Successive measurements for any particular bird will tend to show autocorrelation among the residuals from the Richards curve if they are separated by a short enough time interval. If these residuals are then used as the basis for statistical inference about the data, bias caused by the autocorrelation may undermine the results. The effect could cause confidence intervals based upon the asymptotic covariance matrix to be too narrow. White and Ratti (1977) discussed the autocorrelation problem and proposed ways to correct for the bias. Fortunately, the

problem is relevant only at the third level of sampling (Fig. 1). Thus the separate fit and jackknife approaches presented here evade the problem of autocorrelation by treating each sampling unit as a separate entity.

The second problem (correlation among parameters) has caused difficulties throughout this study. First, it exacerbates the nonlinear regression effort, and in the process, destabilizes the parameter estimates. Interpretation is complicated by the fact that the parameters are not really measuring separate aspects of the growth patterns. The extremely high correlation (.95) between the growth constant (K) and the shape of the curve (M) displayed in Table 1 indicates that these two factors work together to estimate the rate of growth of the birds. They are not separable into independent components. Simultaneous adjustment of these two parameters can yield alternative but very similar curves which fit data nearly equally well. This is at least partly due to the fact that the slope at inflection (R) can remain the same despite changes in shape (M) if corresponding adjustments are made to K.

The close tie between K and M reduces the utility of these values in comparing growth patterns for separate populations since K is not comparable between curves of different shape. The instability will often cause M and its transform (P) to have broad confidence intervals and indicate differences between populations only when their growth curves have a substantially different inflection point. One proposed growth rate measure, R (the slope at inflection) is not affected by indeterminacy in K and M and seems to be a potentially useful rate measure since it indicates the maximal growth rate achieved during the entire growth period. Unfortunately, it depends on the location of the inflection point and thus has limited comparability across curves of different shape. In fact, the only strong association revealed in Table 1 for R is a positive correlation with the time to reach inflection which measures a different percentage of the total growth for curves that differ in shape. The best overall growth measure appears to be the time to pass from 10% to 90% of asymptotic size (G). This has two advantages: 1) it is less affected by instability of the nonlinear fit than K or M, and 2) it produces values on an easily interpreted scale (days or hours).

The asymptote is an alternative measure which seemingly should not be related to the growth rate. However, with the Burrowing Owl data, it showed a substantial negative correlation with K, M, P, and G. This does not appear to be an artifact of the fitting process for the curves, since for the owls, there was plenty of data (30 days) beyond the primary growth period which provided an accurate basis for estimating the true asymptotes.

The techniques for computing confidence intervals described earlier all produce separate univariate intervals for each summary statistic. The extension to multivariate confidence regions is possible, but has shown little success in past work with nonlinear regression (Duncan 1978). It is important to remember that the high intercorrelation among the summary statistics guarantees that corresponding confidence intervals are not independent of each other. For example, if two samples differ substantially on the basis of both asymptotic size and length of the primary growth period, it is incorrect to argue that these samples differ in two independent aspects of their growth pattern. Instead, the two observed differences should be viewed as separate manifestations of a single underlying pattern.

The third problem in fitting Richards' curve arises when data cannot be obtained

beyond the time when the birds reach their asymptotic size. For example, if the birds fledge and disappear as they reach their asymptotes, or if there is weight recession (Ricklefs 1968b) and truncated data must be used to fit the curves, then the asymptote will not be accurately specified by the data (Fletcher 1975). In these cases, it may be necessary to tightly restrict the estimated asymptote to a reasonable range in order to produce acceptable growth curve fits. Perhaps a more effective strategy would be to fix the asymptote *a priori* at an appropriate value such as the adult mean. In any case, with truncated data sets, it will not be generally possible to separate the effects of asymptote and growth rate in determining the curves.

In summary, the general strategy which we have pursued is to provide statistics which measure certain aspects of the observed growth patterns. The Richards curve serves in this context merely as a measuring device (an extension of the spring balance) which extracts these summary statistics from the raw data. Other researchers have explored a different area of application for the Richards growth function: direct modeling of the growth process. Sandland and McGilchrist (1979) and White and Brisbin (1980) have employed stochastic modeling techniques with the Richards curve. In contrast, we do not consider our technique as an appropriate model of the true growth process. Rather, it is merely a way of summarizing growth patterns and comparing separate populations. For this purpose, we recommend use of the duration of the primary growth period (G) and (with adequate data) the asymptotic size (A) as appropriate statistics to describe the growth patterns.

An APL program which performs the growth analyses presented in this paper is available from the lead author upon request. It employs the previously discussed modified Gauss-Newton method for nonlinear regression.

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¹ Department of Data Processing and Information Systems, and ² Department of Biology, California State University, Long Beach, California 90840.

Appendix

Richards original parameterization took the form:

$$W = A(1 \pm Be^{-\frac{1}{KT}(1-M)}) \quad A1$$

where B represented the time scale adjustment. The sign flips from negative when M is less than 1 to positive for M greater than 1. Richards also provided an expression for the weight at the time of inflection:

$$W_i = AM^{\frac{1}{1-M}} \quad A2$$

Substituting the weight at inflection (from equation A2) for W in equation A1, dividing both sides by A and raising both to the $1 - M$ power yields:

$$M = 1 \pm Be^{-KI} \quad A3)$$

where I (the time of inflection) is inserted for T . Solving for B gives:

$$B = (M - 1)e^{KI} \quad A4)$$

Note that in this formulation B is automatically negative when M is less than one and positive otherwise, eliminating the sign ambiguity when B (from equation A4) is substituted for $\pm B$ in equation A1. This substitution results in our form of Richards' curve as expressed by equation 1 in the text.

The calculation of the time from 10% to 90% of asymptotic size begins with the formula for size as a percentage (E) of the asymptote:

$$E = \frac{W}{A} = (1 + (M - 1)e^{-K(T-I)})^{\frac{1}{1-M}} \quad A5)$$

Solving for T in terms of E gives:

$$T = I - \ln(1 - M)/K - \ln(1 - E^{1-M})/K. \quad A6)$$

The time differential from $T_{.10}$ to $T_{.90}$ arises by subtracting equation A6 for $E = .10$ from the formula with $E = .90$:

$$G = [I - \ln(1 - M)/K - \ln(1 - .10^{1-M})/K] - [I - \ln(1 - M)/K - \ln(1 - .90^{1-M})/K]$$

Cancellation and composition yields the final formula for G :

$$G = \ln((1 - .10^{1-M})/(1 - .90^{1-M}))/K.$$

A Recent Specimen of *Collisella edmittchelli* from San Pedro, California (Mollusca: Acmaeidae)

David R. Lindberg

Abstract.—A recent specimen of *Collisella edmittchelli* from San Pedro, California (Mollusca: Acmaeidae) by David R. Lindberg. *Bull. Southern California Acad. Sci.*, 83(3):148-151, 1984. The first known Recent specimen of *Collisella edmittchelli* (Lipps, 1966) is reported. The Recent specimen suggests that some of the fossil specimens' characters are preservational. Fossil specimens also may be present on San Miguel Island. This species may have lived lower in the intertidal region than previously thought.

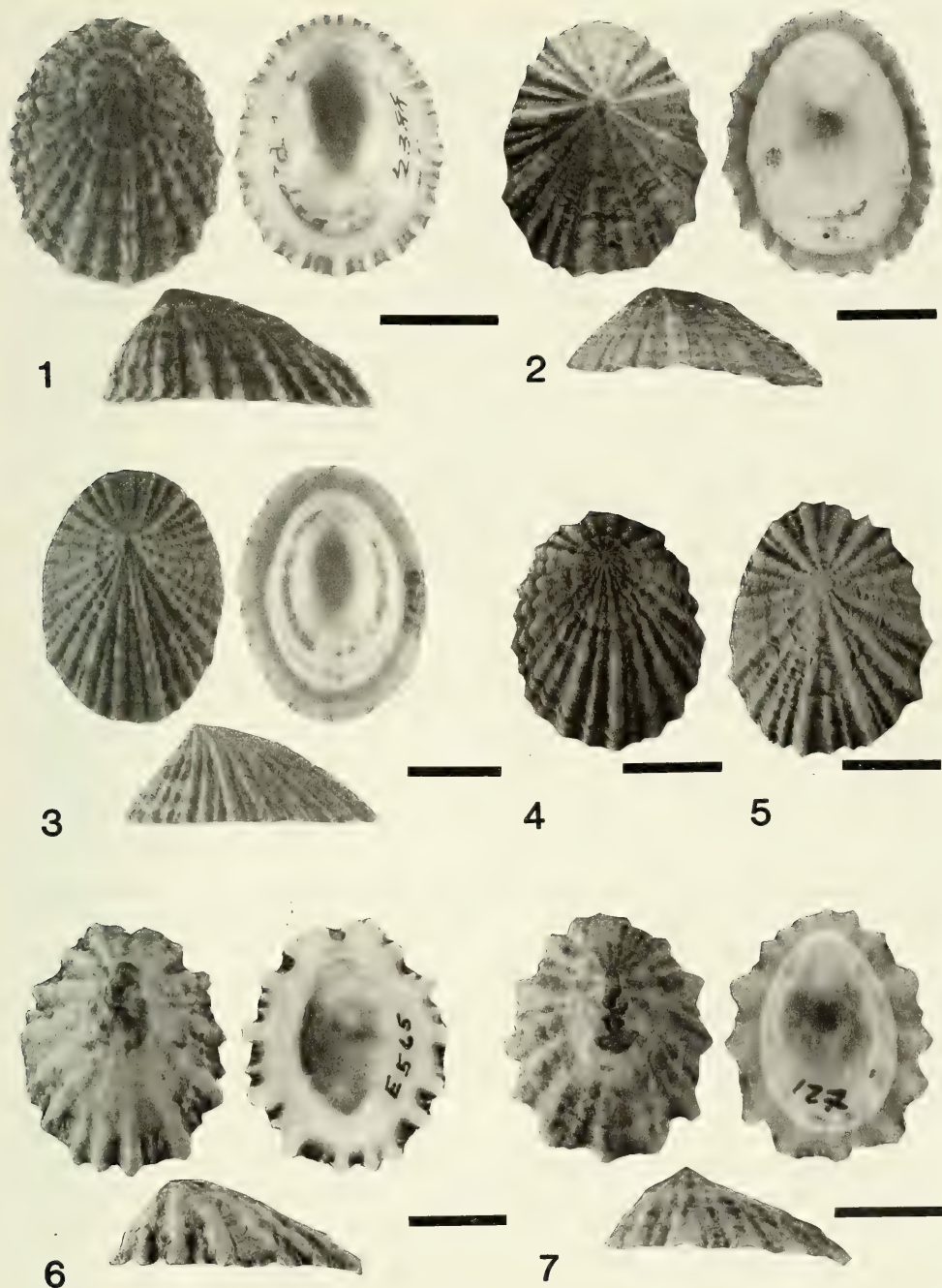
Previously, *Collisella edmittchelli* (Lipps 1966) was the only acmaeid limpet present in the Pleistocene of southern California that was not extant today; it was known only from Pleistocene deposits on San Nicolas Island, Ventura County, California (33°16'N, 119°30'W).

During the summer of 1983, I found a specimen lot identified as *Acmaea spectrum* [= *Collisella scabra* (Gould 1846)] in the collections of the Museum of Paleontology, University of California, Berkeley (UCMP). The specimen lot (UCMP Loc. #2388) had been collected at San Pedro, California by J. G. Cooper and contained three shells, two of which were typical *C. scabra*, but the third specimen was quite different. Further examination of the odd specimen revealed that it is a specimen of *C. edmittchelli*. In addition to the discovery of this Recent specimen of *C. edmittchelli*, study of fossil specimens from several localities on San Nicolas Island has produced additional information on this enigmatic species that is included herein.

Examination of the shell layers, as they appear on the interior surface, revealed that the Recent specimen belongs to MacClintock's (1967) shell structure group no. 16. *Collisella scabra* and *C. edmittchelli* are the only species known to have this shell structure (Lindberg 1978).

The shell morphology of the Recent specimen (Figs. 1, 4) is clearly within the range of variation of *C. edmittchelli* (Figs. 2, 3, 5) and not *C. scabra* (Figs. 6, 7). In *C. scabra*, the radial ribs number between 10 and 20, whereas in *C. edmittchelli* there are between 20 and 30 radial ribs (Lindberg 1978). The Recent specimen has 25 ribs. Moreover, the size of the ribs differs substantially between the two species. In *C. scabra*, the primary ribs are about twice as wide as the secondary ribs. In *C. edmittchelli* the secondary ribs are only slightly narrower than the primary ribs. Overall, the ribbing of the Recent specimen (Fig. 4) is most similar to that of *C. edmittchelli* and not that of *C. scabra* (Figs. 6, 7). Other characters such as the shell profile, the crenulation of the aperture, and the lack of a central stain, all are characteristic of *C. edmittchelli* and not *C. scabra*.

The San Pedro specimen is the only known Recent record of *C. edmittchelli*. Dried mantle tissue along the posterior edge of the muscle scar confirms the Recent



Figs. 1-5. *Collisella edmitcheelli* 1, Recent, San Pedro, California; UCMP 37424. 2, Pleistocene, San Nicolas Island, California; UCMP 37425. 3, Holotype, San Nicolas Island, LACMIP 1126. 4, UCMP 37424 coated with ammonium chloride. 5, UCMP 37425 coated with ammonium chloride.

Figs. 6-7. *Collisella scabra* 6, Recent, Santa Catalina Island, California; UCMP 37426. 7, Pleistocene, San Nicolas Island; UCMP 37427. Scales = 10 mm.

nature of the specimen. It also is the first record of *C. edmitchelli* outside of San Nicolas Island.

The locality and collection date are accurate, Coan (1981) places J. G. Cooper at San Pedro, California in 1861 and again in 1863. Collections were made on both occasions. Evidence that Cooper collected the specimen comes from several labels with the specimen and the entry in the UCMP locality register. Moreover, on the interior of the specimen are the words "San Pedro" (Fig. 1). Similar locality names, written in Cooper's hand, are on other specimens collected by him from Southeast Farallon Island and Santa Barbara.

The Recent specimen of *C. edmitchelli* significantly increases our knowledge of this species. Lipps (1963) considered the dark interior margin of *C. edmitchelli* (Figs. 2, 3) to be a diagnostic character of the species. However, it now appears that this character is a product of diagenesis. The outer modified foliated shell layer is glossy white in the Recent specimen but brown in Pleistocene specimens. The same change occurs in the outer layer of *C. scabra* (Figs. 6, 7).

Another important character, the lack of the central stain, is a feature of the Recent specimen. *C. scabra* has an irregular, dark brown central stain (Fig. 6) but *C. edmitchelli* lacks a stain (Figs. 2, 3). The lack of a central stain is a conservative character and not preservational. The Recent and fossil specimens of *C. edmitchelli* (Figs. 1, 3), lack a central stain. In *C. scabra*, an irregularly-shaped stain is present on Recent and fossil specimens (Figs. 6, 7).

The restriction of fossil specimens of *C. edmitchelli* to San Nicolas Island and the unique occurrence of a Recent specimen at San Pedro is puzzling. On San Nicolas Island, *C. edmitchelli* is abundant on the higher terraces (terraces 11 through 5 of Vedder and Norris 1963). These terraces are between $770,000 \pm 100,000$ yrs BP and $400,000 \pm 100,000$ yrs BP (Lajoie, Wehmiller, and Kennedy 1980; G. L. Kennedy, pers. comm.). Other acmaeid limpets occurring with *C. edmitchelli* include *Collisella limatula*, *C. digitalis*, *C. pelta*, and *Acmaea mitra* (Vedder and Norris 1963). At most localities *C. limatula* is the most abundant followed by *A. mitra* and *C. edmitchelli* (D. R. Lindberg, unpublished data). *C. scabra* is absent from the higher terraces and is abundant only on terraces 1–4.

C. edmitchelli may also be present in the higher terraces on San Miguel (34°3'N, 120°21'W). Cockerell (1938:9) reported limpets from the high terraces of the island that were an "extreme variant" of *C. scabra*. Specimens of *C. edmitchelli* could certainly be mistaken for an "extreme variant" of *C. scabra*. Unfortunately these specimens could not be located.

Lipps (1963), using shell morphology, postulated that *C. edmitchelli* was a high intertidal species. However, one specimen (Fig. 2) has been drilled by a predatory gastropod. The borehole in the posterior region of the shell is similar to those produced by the muricid gastropod *Nucella* in the Recent San Nicolas fauna. *Nucella* also occurs in some of the same terrace deposits as *C. edmitchelli*. Discounting the possibility of physiological changes in *Nucella* spp., and the possibility that the snail drilled an empty limpet shell, and the habitat suggested by the Recent intertidal range of *Nucella* spp. would suggest that *C. edmitchelli* occurred in the mid-intertidal region rather than the high intertidal. *C. scabra* reaches its highest densities in the mid-intertidal region on San Nicolas Island today (Estes and Lindberg, in preparation).

No other Recent specimen of *C. edmitchelli* was found in the collections of

UCMP, the California Academy of Sciences, or the Natural History Museum of Los Angeles County. However, the presence of this species during the 1860's at San Pedro, California suggests that additional specimens may be extant, possibly in older collections.

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Museum of Paleontology, University of California, Berkeley, California 94720.

Research Notes

Observations of Harbor Seal, *Phoca vitulina richardsi* Feeding in Southern California Waters

Although the diet of the harbor seal, *Phoca vitulina richardsi*, has been described for many areas, little is known of the diet in southern California waters. Harbor seals from northern California to Alaska are generally opportunistic feeders. Their diet varies with season and location and includes pelagic, benthic, and anadromous fishes, as well as molluscs and crustaceans (Spalding 1964; Kenyon 1965; Pitcher 1980a,b; Antonelis and Fiscus 1980; Jones 1981).

Additionally, little is known of the feeding behavior of harbor seals. Hobson (1966) noted that night feeding harbor seals swam on their backs and approached pelagic prey from below. This would be advantageous in that the prey is silhouetted against the water surface by the light, even starlight, coming from above. This note describes feeding behavior of harbor seals observed off the southern California Channel Islands and reports a new prey species.

On 20 October 1982, between 2050 to 2110 hours, we made a night SCUBA dive at Eagle Reef, a rocky pinnacle offshore of Lion Head Point, near Isthmus Harbor, Santa Catalina Island. Dive depths were 7.6 to 10.7 m and water visibility was estimated at greater than 10 m. Each of us carried a bright underwater flashlight (Underwater Kinetics SE 200).

Eagle Reef includes several pinnacles bordered by shelves and flat rocky reef areas with many crevices and shallow undercuts. The blacksmith, *Chromis punctipinnis*, a nocturnally inactive pomacentrid fish, uses such cracks and crevices for night-time shelter (Hobson et al. 1981).

A harbor seal first appeared early in the dive, swimming under us in a supine attitude. During the first encounters, the seal circled, then brushed two of us (D.O.P. and K.C.H.). Still in an inverted position, the seal proceeded to a shallow crevice and began probing along it with its muzzle. Whenever it approached a blacksmith, the seal would stop momentarily, then dart at the fish, often catching it. We observed this behavior repeatedly during the dive. Apparently the seal swallowed the fish underwater as it once captured several blacksmith on a single dive.

On the night of 15 December 1982, two of us (P.L.H. and D.O.P.) returned to Eagle Reef. Another, smaller harbor seal was observed feeding as described above. During this encounter, the seal released the almost separated halves of a blacksmith, bit the head, and swallowed the fish head first. During feeding dives this seal swam in both a supine and a prone attitude.

On 8 March 1977, Jack Engle and Tim Tricas (pers. comm.) of the University of Southern California Catalina Marine Science Center made a night dive at Ship Rock, also near Isthmus Harbor, Santa Catalina Island. The dive began at 2245 hours and covered waters to 10 m deep. The divers observed "Fish Hook," a somewhat tame harbor seal foraging in "every conceivable crevice." Engle noted that "away from the range of our lights, he seemed to be catching blacksmith by

touch. With the aid of our lights he could see to dart out at fleeing blacksmith. Usually he bit the fish immediately upon contact, then pulled back and readjusted it for swallowing head first." This behavior was observed over a 45 minute period, during which "Fish Hook" ate 20 or more blacksmith. Tim Tricas also saw the seal eat a blackperch, *Embiotoca jacksoni*, which was lying in low-growing algae.

On 10 October 1982, at about 2100 hours, Todd Tognazzini (pers. comm.), a National Park Service Ranger, observed a harbor seal pursuing fishes beneath rock ledges in 6.5 to 7.6 m deep water off Middle Canyon at Santa Barbara Island. The seal forced its body under ledges and churned up substrate as it attempted to swim deeper into the crevice. The seal removed itself from the crevice, turned from the light, and swam away. It could not be determined what prey, if any, had been taken.

Blacksmith are commonly seen during the day in large schools around kelp forests. They appear to be sufficiently abundant to be an important prey item in the diet of *P. vitulina*. At night, when taking shelter in crevices, blacksmith are probably more susceptible to seal predation. However, we cannot say whether the behavior observed above is normal or just an artifact of the presence of artificial illumination. If such behavior is normal for the species, other fishes having similar nocturnal habits as that of the blacksmith, may also be susceptible to predation by harbor seals.

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Peter L. Haaker, David O. Parker, and Kristine C. Henderson, *California Department of Fish and Game, 1301 West 12th Street, Long Beach, California 90813.*

Two Species of *Lytechinus* (Toxopneustidae: Echinoidea: Echinodermata) Are Completely Cross-fertile

The sympatric sea urchins, *Lytechinus anamesus* Clark 1912 and *L. pictus* (Verrill, 1867) are found in different microhabitats. *L. anamesus* primarily resides in open coast areas, while *L. pictus* is found in bays and lagoons (Ricketts and Calvin 1968; T. A. Ebert, S. Schroeter and others, pers comm.). Although Mortensen (1943) considered the two forms to be valid species, Mayr (1954) omitted *L. pictus* from his zoogeographical discussion of the genus because he thought it was possibly a synonym of *L. anamesus*. A key to the species of the genus distinguishes between the two forms on the morphology of the spicules found in the stalk of the globiferous pedicellariae (Chesher 1968). Word and Charwat (1975) separate the two species in their key on the basis of spine morphology and color. Furthermore, the two forms are readily cross-fertilizable and embryonic cells will reaggregate to produce viable early embryos (Vacquier, quoted in Durham et al. 1980).

The observations above could be accounted for by one of at least two hypotheses. The two forms could be ecotypic variants within a single species or truly isolated populations between which no genetic exchange occurs. In order to exclude the isolation hypothesis, it must be shown that: (1) the hybrids can successfully develop and survive to the adult form and (2) exchange of gametes or larvae can occur in nature. The tests for development and survival can be easily accomplished since techniques for larval rearing are readily available (Hinegardner 1969; Cameron and Hinegardner 1974).

Materials and Methods

Adults obtained from Mission Bay, San Diego, California, and off San Onofre, California were maintained in running seawater at the Long Marine Laboratory, University of California, Santa Cruz. Observations were made on these animals as well as laboratory reared populations of unknown pedigree.

To test for larval survival, reciprocal crosses between the *L. pictus* and *L. anamesus* were made. Gametes were obtained by injection of 0.55 M KCl through the peristomial membrane. Eggs from each female were separately collected in filtered seawater and semen was collected undiluted on ice. Fertilization was accomplished by mixing 10 ml of a 10% egg suspension with a few drops of a 1% suspension of semen. After thorough washing to remove sperms, fertilized eggs were diluted and maintained at 18 degrees C.

At two days post-fertilization, the embryos were diluted to one per 15 ml and placed in stirred culture vessels (Cameron and Hinegardner 1974). The cultures were fed a unicellular cryptophyte, *Rhodomonas lens*, which was kept at approximately 3000 cells/ml by daily inspection. Mature larvae were challenged to settle by placing them in plastic petri dishes which had acquired a bacterial film while lying in aquariums containing adult urchins.

Random aliquots of seawater from vigorously stirred cultures containing embryos or larvae were transferred at each succeeding culture step in order to prevent unwitting selection of particularly healthy individuals.

Embryos and larvae were examined using a Baush & Lomb dissecting microscope and a Zeiss compound microscope with phase and Nomarski optics. Observations were made on the following schedule:

Time after fertilization	Event scored	Total observed
2 hrs	cleavage	800
2 d	gut development	4000
49 d	general appearance	5153
	metamorphosis	

Results

Using the criteria of pedicellarial stalk spicule morphology described by Chesher (1968), I was unable to separate the two species. The forms of the spicules graded from club-shaped to hooked regardless of the type observed. Based on the external features of spine length and test color used by Word and Charwat (1975), the two species are easily separated.

Because the two forms of *Lytechinus* freely interbreed and produce embryos under laboratory conditions, developmental biologists have used them extensively without considering the species differences. Offspring from inadvertent mixing of the two forms have been reared to sexual maturity without regard to pedigree. They assume the form of *L. anamesus* in the wild. They have longer light-colored spines and a whitish test blotched with purple. A gradation in form from dumbbell- to C-shaped pedicellarial spicules is also evident.

After two hours of development, 80% or more had completed at least one cleavage (Table 1). Some had progressed to the four-cell stage.

Table 1. Percent of zygotes exhibiting cleavage furrows at two hours after fertilization. Estimates based on state of 200 eggs for each cross.

	♀ <i>anamesus</i>	♀ <i>pictus</i>
♂ <i>anamesus</i>	89%	99%
♂ <i>pictus</i>	92%	94%

The appearance of the early plutei which were transferred to feeding cultures was also the same among the four groups. At each weekly water change, no difference in growth or development was observed between any of the four groups of larvae. After 49 days in culture the larvae appeared mature and competent to undergo metamorphosis. Of the 2153 individuals scored in all the crosses, 87% or more had undergone the rapid events of metamorphosis and begun to develop adult structures (Table 2).

Discussion

These experiments indicate that the integrity of these species is not maintained by a barrier to successful larval development. In all crosses, the eggs cleaved

Table 2. Percent of larvae from each cross which successfully completed metamorphosis.

$\delta \times \text{♀}$	Percent metamorphosis	Number
<i>anamesus</i> $\times$ <i>anamesus</i>	97	526
<i>pictus</i> $\times$ <i>pictus</i>	93	364
<i>anamesus</i> $\times$ <i>pictus</i>	93	475
<i>pictus</i> $\times$ <i>anamesus</i>	87	788

successfully and the embryos developed normally within the limits of the sea urchin culture techniques (Hinegardner 1969; Cameron and Hinegardner 1974). The percents of metamorphosis were within a normal range for all the crosses also. From these investigations it is clear that no barrier to cross breeding or intertypic larval development exists. Therefore, isolation of these populations could result from difference in settlement, juvenile survival or larval and gametic transport. Since the intratypic matings settled successfully in the laboratory, it is reasonable to assume that substrate selection is the least likely isolation mechanism. It is also probable that the larvae of each form would occasionally find their way into the habitat of the congener. Perhaps after settlement juveniles cannot survive in the contratypic habitat.

Morphological variation of the same magnitude as seen in *Lytechinus* has been documented in the latitudinally broad ranging sea urchin, *Arbacia punctulata*. In addition, the genetic variation between populations of this species has been inferred from protein variation (Marcus 1977). Although the gene frequencies were significantly different between populations, the overall values calculated for gene distance were within the range observed for geographical populations of other species. Both migration accomplished by larval transport and selection have been proposed to account for the differences in gene frequency. While the selection factors were implied to be physical ones, no data is available on this question.

Interspecific hybrids of sea urchins have been reported many times (see Harvey 1956 and Giudice 1973 for review). Hybrids between the purple sea urchin, *Strongylocentrotus purpuratus*, and the red sea urchin, *S. franciscanus* are of particular interest because they are a co-occurring pair of congeneric species found within the range of the *Lytechinus* forms. Crosses between untreated purple sea urchin eggs and red sea urchin sperms yielded as high as 18% fertilization while reciprocal crosses yielded 9% (Chaffee and Mazia 1963). These levels were accomplished by adding large amounts of sperms to a concentrated egg suspension. They can be regarded as unusually high yields, generally the percent of fertilization is much less (Hinegardner 1967). In these experiments development was only observed until the pluteus stage (72 hr). It is not known if the hybrids would develop normally to metamorphosis. Because the levels of fertilization in reciprocal crosses described here have always exceeded 90%, it is more likely that these forms are not separate species, unlike the *Strongylocentrotus* case. However, before these species can be combined, other critical tests must be made. For example, do real barriers to migration or gamete exchange exist; i.e., is hybridization possible in the field. The *Lytechinus* forms may simply be ecotypic variants. This hypothesis has not been examined here. The best test of the hypothesis would be transplantation of young adults from one habitat to the other with observations on changes in spine length and test color over a period of time. Recently it has

been shown that *Strongylocentrotus drobachiensis* and *S. pallidus* can produce viable hybrids in the laboratory. In nature, the species probably remain distinct because of sufficient selection against hybrids (Strathmann 1981).

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Dr. R. Andrew Cameron, *Department of Marine Sciences, University of Puerto Rico, Mayaguez, Puerto Rico 00708.*

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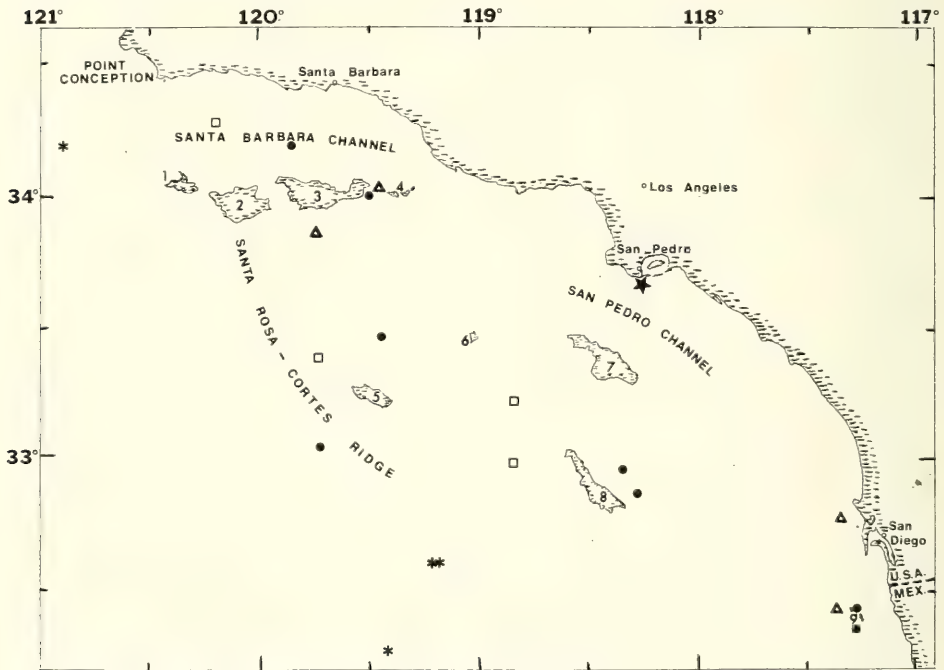
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Humpback Whale (*Megaptera novaeangliae*) Sighting off Los Angeles Harbor, Southern California

Humpback whales, *Megaptera novaeangliae*, are found in all oceans. In the Northern Hemisphere they migrate from southern winter grounds to northern summer feeding grounds. They follow no clear-cut migration routes, and the boundaries of their summer and winter grounds are uncertain. No sightings of this species in the San Pedro Channel have been reported to date. Data are presented here on a nearshore sighting of *M. novaeangliae* off the San Pedro area

on 5 May 1982. The whale's distinctive scars and disfigurations may enable its migration movements to be traced.

Severe whaling pressures have reduced the world humpback population to 6000–7000 animals (Anonymous 1982). The North Pacific population, about 1000 whales (Leatherwood et al. 1982), migrates from mostly Arctic waters to three main wintering sites. Over 650 humpbacks migrate to the Hawaiian Islands, 100–200 to Mexico, and a small, undetermined number, to island waters off Asia. Information concerning migration routes and site fidelity has been largely determined from the tracking or capture of whales with implanted tags. Another method utilizes photographic identification based on natural tags such as color patterns and shapes of flukes and dorsal fins. Photo-identification systems have been computerized for both North Pacific and North Atlantic humpback whale populations (Anonymous 1982; Katona et al. 1981). Until a few years ago, most researchers believed that “Mexican” humpback whales summered off southern Alaska and “Hawaiian” humpbacks migrated to the Aleutian Islands. Photo-documentation has established that at least part of these two “stocks” share feeding grounds in southeastern Alaska (Lawton et al. 1979; Payne 1982). Photographs also depict some whales migrating to Hawaii one summer and to Mexico the next, thus merging the breeding stocks (Payne 1982).



LEGEND

SIGHTINGS BY MONTH: JANUARY-MARCH (Δ); APRIL-JUNE (*); MAY, 1982 ($\star$); JULY-SEPTEMBER ($\bullet$); OCTOBER-DECEMBER ($\square$).

ISLANDS: SAN MIGUEL (1); SANTA ROSA (2); SANTA CRUZ (3); ANACAPA (4); SAN NICOLAS (5); SANTA BARBARA (6); SANTA CATALINA (7); SAN CLEMENTE (8); LOS CORONADOS (9).

Fig. 1. *Megaptera novaeangliae* sightings from 1949–1978, and 1982 sighting, in the southern California Bight.



Fig. 2. *M. novaeangliae* surfacing near the Los Angeles Breakwater. Rostrum is at A, and nares at B.

Humpback whales are regularly sighted in their eastern North Pacific winter grounds October through May. Mexican grounds extend south along the west coast of Baja California and around the peninsula into the Gulf of California north to at least San José Island. According to Leatherwood et al. (1982), the summer grounds extend from the Bering Sea south to Point Conception. Rice (1974) maintained that many sightings occur throughout the summer off central California. For the last five years, Woodhouse (pers. comm.) has recorded annual sightings of 20–30 whales in the Santa Barbara Channel between May and September. A Bureau of Land Management (BLM) survey (Norris et al. 1976, 1981) summarized 28 humpback whale sightings reported from Point Conception to the Mexican border between 1949 and 1978. Most whales were sighted from June to November in water 90 to 1500 m deep. The study concluded that the Santa Barbara Channel appears to be a humpback whale seasonal gathering ground, and the Santa Rosa-Cortes Ridge may be a major migratory pathway. No sightings have been reported from the San Pedro Channel. The 1982 sighting documented below is incorporated with BLM sighting data in Figure 1.

While conducting marine biology classes for Los Angeles school children, the vessel *DAIWA* sighted a single whale at 1330 h on 5 May 1982. Three other vessels engaged in similar activities joined the first: the *MAVERICK*, the *AT-LANTIS*, and the *GOLDEN DOUBLOON*. The following observations took place from the *GOLDEN DOUBLOON*. Calm sea conditions and clear photographs aided verification of the whale's identity as a humpback.



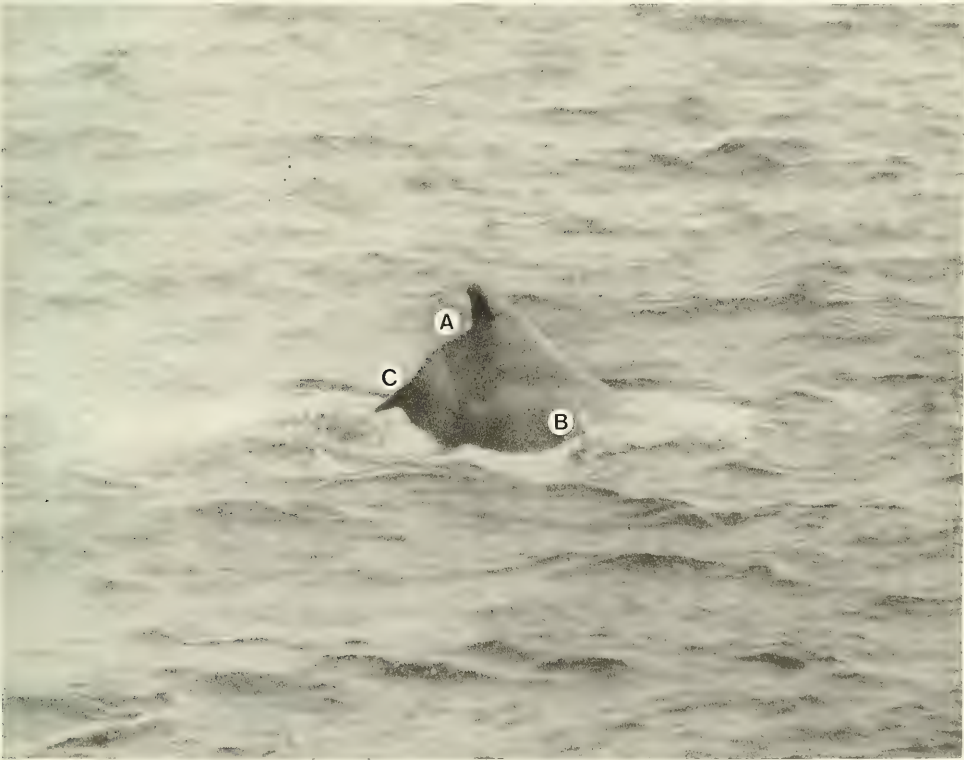
Fig. 3. *M. novaeangliae* surfacing in kelp, with scars at A and B, and deformation posterior to dorsal fin at C.

The whale was initially sighted at latitude $33^{\circ}42.4'N$ and longitude $118^{\circ}15.1'W$. At this time it was swimming near the Los Angeles Harbor entrance (Angel's Gate), less than 50 m from the breakwater (Fig. 2). The vessel stayed with the whale for 5.6 km, last sighting it at $33^{\circ}41.8'N$ and $118^{\circ}19.4'W$ at 1445 h. The whale's size was estimated at 12.5–13.5 m. Water depth varied from 18 to 22 m during most of the encounter, but had increased to 50 m when contact broke off. The whale's proximity to shore ranged from 0.5 to 3.5 km. It surfaced as close as 15 m from the vessel, enabling detailed observations of scars and prominent deformation posterior to the dorsal fin. Traveling 6.5 to 7.5 km/h, it typically blew three to five times, and then made a short dive lasting between 2 and 4 min.

The whale usually came up blowhole first, slowly arching with apparent torquing of its trunk to the right, and dove without raising its flukes. The dark dorsal surface of the flukes was glimpsed only once. Either the relatively shallow water traversed by the whale during the observation period or the presence of a back injury could have accounted for the lack of characteristic fluking behavior. The pectoral fins were never observed. The water's high plankton content, combined with the boat's low viewing angle, limited the underwater visibility to about 3 m.

→

Figs. 4a and 4b. Dive sequence showing view of whale's right side, with scars at A and B, and deformation posterior to dorsal fin at C.



The rostrum showed clearly twice. The first time followed a relatively long dive (Fig. 2). The second display occurred when the whale raised its head through the sole patch of giant kelp (*Macrocystis pyrifera*) in its path. The humpback paused, draped in seaweed, and then moved through the fronds (Fig. 3). Rostral tubercles showed distinctly, as did an apparently healed injury (A, B, and C) illustrated in Figures 3 and 4. A small white scar (A) is visible at the posterior base of the dorsal fin. These figures also indicate the presence of at least six fairly parallel scars (B) below the dorsal fin on the right side. The dorsal ridge posterior to the fin is s-shaped, a feature which produced laterally distorted ridge bulges (C). The parallel nature of the scars, and their relative position to the spinal deformation, suggest that this injury may have been the result of a collision with a boat.

In addition to identifying a distinctly marked individual in an area from which no previous encounters have been reported, this shallow water sighting is significant because of the paucity of published data concerning the humpback whale's migration movements. The unusual individual documented here can be readily identified by features other than its flukes, which will ease tracking of its movements and behavior among other whales. If it regularly winters in Mexican waters, the small number of neighboring whales increase its chances of being resighted. Evidence provided by resightings will add to knowledge concerning migration routes, seasonal range parameters, and perhaps even population crossovers.

Acknowledgments

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Alisa Schulman, *Sea Education Afloat (SEA) Instructor, San Pedro Science Center, 2201 Barrywood Ave., San Pedro, California 90731.*

A New Genus and Species of Iphitimid Parasitic in an Aphroditid (Polychaeta), with an Emendation of the Family Iphitimidae

Endoparasitic polychaetes taken from the coelomic cavity of *Aphrodita longipalpa* Essenberg are herein described as a new genus and species of the Iphitimidae. The familial definition of the Iphitimidae is therefore emended to encompass the new genus. Type materials are deposited at the Allan Hancock Foundation (AHF), University of Southern California, Los Angeles, California.

Family Iphitimidae Fauchald, 1970, emended
[Type genus: *Iphitime* Marenzeller, 1902]
Iphitimidae Fauchald, 1970:118 (By monotypy)
Iphitimidae: Pilger, 1971:84 (emended)

Familial diagnosis.—Prostomium short, rounded or truncate; 1 pair of frontal antennae present or absent. Peristomium up to 2 segments long. Parapodia uniramous; 1–8 acicula present per parapodium. Pharyngeal apparatus with 1–3 pairs of maxillae; 1 pair of short maxillary carriers fused to falcate maxillae I; third maxillary carrier absent. Mandibles present; partially to completely fused medially. Setae including simple or compound falcigers, all without distal hoods.

Generic diagnosis.—Body long and slender, ventrally flattened; branchiae absent. Prostomium without antennae. Two peristomial segments, each apodous, lacking cirri. Parapodial lobes simple, uniramous. Setae of one kind, entirely simple. Pharyngeal apparatus with one pair of maxillae, these fused basally with carriers, these fused together medially. Mandibles completely fused medially into a single oblong structure.

Remarks.—This new genus is included in the Iphitimidae since the maxillary carriers are basally fused to maxillae I. This character is atypical of other families of the Eunicida, although it may be present in dorvilleids (Fauchald 1970). *Veneriserva* resembles *Iphitime* only in body form, lacking both branchiae and peristomial appendages. *Veneriserva* has only 1 pair of maxillae while *Iphitime* has 2–3 pairs. The fusion of the mandibles into a single oblong structure is unique to *Veneriserva*.

Etymology.—The generic name (*venerius*, Latin = of or pertaining to Venus; *serva*, Latin = servant) refers to the close association with an *Aphrodita*.

Veneriserva pygoclava, n. sp.

Fig. 1a–f

Material examined.—A total of 8 specimens as follows: Holotype (AHF 1275) and 3 paratypes (AHF 1276) taken from an *A. longipalpa* collected at Southern California Coastal Water Research Project (SCCWRP) trawl station C-10 (33°31.5'N, 118°13.7'W; 457 m; July 1976); 4 specimens from another *A. lon-*

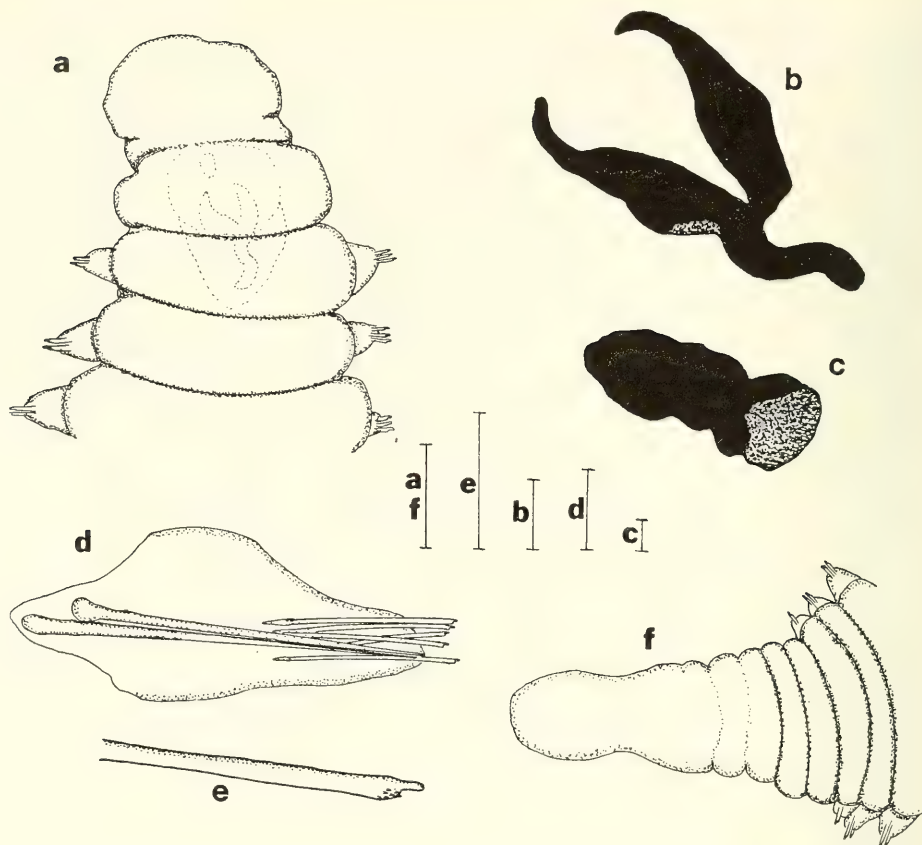


Fig. 1. *Veneriserva pygoclava* n. sp.—a, anterior end, dorsal view; b, maxillae I and carriers; c, mandibles; d, median parapodium; e, seta; f, pygidium, dorsal view. (Scale a, f = 0.25 mm; e = 0.04 mm; b = 0.05 mm; d = 0.1 mm; c = 0.01 mm.)

gipalpa collected at SCCWRP trawl station L-1500 (33°30.5'N, 117°47.7'W; 457 m; Nov. 1976).

Description.—Length of holotype 18 mm, width maximally 1 mm, with 205 segments; largest paratype (♀) 35 mm long with 400 segments; colorless in alcohol. Prostomium (Fig. 1a) irregularly rounded, ventrally flattened; eyes absent. Peristomial segment 1 short, fused dorsally with prostomium; second peristomial segment a complete ring, three times longer than the first. Maxillae I (Fig. 1b) smooth, thick and distally falcate. Maxillary carriers sigmoidally curved (Fig. 1b). Fused mandibles small, longer than wide (Fig. 1c). Parapodia (Fig. 1d) each with 2 acicula. Setae with slightly curved shafts and a subdistally inflated, minutely spinous boss terminating in a digitiform tip (Fig. 1e); number 4–5 per parapodium. Body tapering posteriorly, terminating in a small club shaped pygidium (Fig. 1f).

Remarks.—This record is the first report of an iphitimid as a polychaete endoparasite. It is also the first record of an aphroditid parasitized by another polychaete. The Iphitimidae, as originally defined, were exclusively associated

either in the branchial cavity (5 species) or under the tail (1 species) of decapod crustaceans (Pilger 1971; Kirkegaard 1977). Previous records of polychaete endoparasitism show that only 13 species of arabellids parasitize other polychaetes. The known host families include the cirratulids, eunicids, nereids, onuphids, terebellids, trichobranchiids, serpulids, spionids, and syllids (Clark 1956; Pettibone 1957; Eliason 1962; Emerson 1974; Amaral 1977).

The parasitism of one polychaete by another is a poorly known phenomenon due in part to its rare occurrence. Direct observations on such fundamental questions as to methods of reproduction, feeding, and host entry are apparently not reported in the literature. Little can be inferred regarding these questions as most parasitic arabellids show little or no structural modifications when compared to free living species. A few species, however, exhibit some morphological modifications. The most aberrant parasitic arabellid, *Haematocleptes terebelledis* Wiren, shows considerably morphological convergence with *Veneriserva pygoclava*. For example, the mandibles and maxillary apparatus are extremely reduced, and the reduced parapodia of *Veneriserva* have minute setae while those of *Haematocleptes* lack emergent setae. Basically these species exhibit the reduction or loss of mouthparts and locomotive structures usually associated with the adoption of an endoparasitic mode of existence.

Sexually mature parasitic arabellids have not been recorded in the literature (Clark 1956). This and the seeming lack of morphological modification has led some observers to note that most endoparasitic arabellids may represent transitory stages in the development of free living adults (Clark 1956; Emerson 1974). The presence of gametes in *V. pygoclava* (eggs observed in one specimen) coupled with obvious morphological adaptations suggests a more obligate form of parasitism.

Etymology.—The specific name (*pygē*, Greek = buttocks; *clava*, Latin = club) refers to the shape of the pygidium.

Ecology.—The method of host penetration is unknown. *V. pygoclava* were found in the ventral and lateral coelomic spaces of the hosts. No penetration of either the gut or gut diverticulae was observed. The method of feeding is unknown.

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Mark M. Rossi, *Dale Straughan International, 7015 Marcelle Street, Paramount, California 90723.*

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Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54:452–458.

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COVER: Postfire skeletal remains of manzanita, *Arctostaphylos glauca*. Photo by Jon E. Keeley.